BIOGEOGRAPHY AND BIODIVERSITY OF STOMIID FISHES IN THE NORTH ATLANTIC

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To my father Jorge
and mother Manuela
To my wife and daughters
Anabela, Beatriz and Leonor

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Abstract

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Filipe J. M. M Porteiro

This thesis intends to improve the knowledge on the biogeography and biodiversity of the North Atlantic midwater environment. The fish family Stomiidae was chosen as a proxy. Theoretical issues and the progress of pelagic biogeography/ biodiversity were reviewed (Chapter 1).

The bulk of the data (87%) came from ichthyological collections. A total of 8185 net-hauls, carried out at 5832 stations produced 141 species distributed by 19727 records, which represent at least 57000 individuals. Net-hauls were classified to a 5º per 5º latitude/ longitude spatial grid and to the Longhurst's eco-biogeographic system (Chapter 2).

Midwater sampling gears and methodologies were inventoried. Among 150 sampling gears, 20 were selected for further analysis. Cruise data and catch related variables were compared. A standard haul was computed for each gear. Commercial trawls sampled largest fish, more individuals, biomass and species per hour of fishing than micronekton and plankton trawls. Comparisons between catches undertaken by the selected gears allow to a computation of a relative net-score. The net-score were scaled in relation to the gear that ranked lower that assumed a value 1. The Engel trawl 1600 ranked first followed by other commercial trawls, large and standard micronekton and plankton trawls. The standardised fishing effort produced by a net-haul was estimated by multiplying fishing time by the net-score. The geographical distribution of the effort undertaken to produce the fish studied was mapped (Chapter 3 and 4).

The Stomiidae ranks amongst the most diverse fish families. Its systematics is acceptably known. This family comprises 26 genera and about 270 species (24 and 141 in the North Atlantic). Fink's Stomiidae phylogeny was used. In the North Atlantic Melanostomiinae is the most speciose sub-family. The derived *Eustomias* is the most species rich genus. Only the genera *Odontostomias* and *Chirostomias* are endemics in the Atlantic. A checklist of North Atlantic Stomiidae species is provided (Chapter 5; Appendix E).

An Atlas of North Atlantic Stomiidae was compiled. Data on relative abundances were used in combination with maps to classify the species in distribution patterns and sub-patterns. Twenty-two patterns and 54 sub-patterns were described: 8 include species that show relatively coherent distributions and were defined without any sub-partitioning; others are complex and have been subdivided in several sub-patterns. Most species fitted to Equatorial, Eastern Tropical Equatorial, Caribbean distant neritic and Subtropical patterns. Expatriation is a common phenomen. Several species have more than one centre of abundance (i.e. mosaic species). Some of those demographic units connect through narrow corridors; others are apparently isolated and were classified as metapopulations. The faunistic relationships between the Longhurst provinces were depicted from multivariate analysis. A sequence from equatorial to polar seas was obtained. The NATR province was split in NATR, NATR E and NATR W. The role of the general circulation on species distribution was discussed (Chapter 6).

The diversity of Stomiid fish was studied using various methodologies (e.g. relative abundance plots, univariate biodiversity indices and multivariate analysis). The highest diversity was found at NAST W, CARB, WTRA and NATR E. ETRA and CNRY had relatively low species richness, similar to NADR. The provinces of the Trade Wind Biome had higher equitability and evenness contrasting to the boreal provinces where dominance was important. The assemblage comprises 31.9% of endemics species plus 25.5% that maintain North Atlantic disjunct populations. High numbers of North Atlantic endemic species occur in the western sector of the subtropical belt, in the Caribbean and the eastern tropical Atlantic. The central oligotrophic and stable water mass (NATR) creates a void in Stomiidae species richness and only a few slender species are abundant in the region. Intermediate levels of seasonal variability (and disturbance) associated with a moderate levels of production seem to be the ideal biotopes for midwater top predators fishes, such as the Stomiidae, to became highly speciose (Chapter 7).

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List of Acronyms

Database and analysis

S_db – Stomiidae database

field_code – the sampling unit; the same as net-haul

sq_5x5 – Areal square of 5º per 5º latitude/longitude

Lgh_P – Provinces of Longhurst's (1995, 1998b) system

Lgh_B– Biomes of Longhurst's (1995, 1998b) system

n_spec – number of specimens

avg_sz – average size

min_sz – minimum size

max_sz – maximum size

avg_wt – average weight

CPUE n – capture per unit effort in numbers (*fish/h*)

CPUE wt – capture per unit effort in biomass (*g/h*)

sp_h – number of species caught per hour

%L – number of species caught in relation to the total provincial assemblage (%)

std_h – standard hours of fishing

t_fishg – time fishing (tow length)

n_spec/std_h – relative density; number of species per standard hour of fishing

Ecological Geography of the Sea (Longhurst, 1995, 1998a,b)

North Atlantic Biomes and Provinces

ATWB - Trade Wind Biome

ETRA - Eastern Tropical Atlantic

WTRA - Western Tropical Atlantic

NATR - North Atlantic Tropical Gyral

CARB - Caribbean

AWWB - Westerly Winds Biome

NAST W - North Atlantic Subtropical Gyral West

NAST E - North Atlantic Subtropical Gyral East
GFST - Gulf Stream
NADR - North Atlantic Drift
MEDI - Mediterranean
APB - Polar Biome
SARC - Atlantic Subarctic
ARCT - Atlantic Arctic
BPLR - Boreal Polar
ACB - Coastal Biome
GUIN - Guinean Current
GUIA - Guianas
CNRY – Canaries
NECS - Northeast Atlantic Shelves
NWCS - Northwest Atlantic shelves

Museum of Natural History and other ichthyological collections

AMNH - American Museum of Natural History, USA
ARC - Hunstman Marine Science Centre, Atlantic Reference Centre, Canada
BMNH - Natural History Museum, London, UK
CAS - California Academy of Sciences, Department of Ichthyology, USA
DOP - University of the Azores, Department of Oceanography and Fisheries, Azores, Portugal
FMNH - Field Museum of Natural History, Division of Fishes, USA
GCRL - Gulf Coast Research Laboratory Museum, USA
IORAS - P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Russia
KU - University of Kansas, Museum of Natural History, USA
MCZ - Harvard University, Museum of Comparative Zoology, USA
MMF - Museu Municipal do Funchal, Madeira, Portugal
MNHN - Museé National d'Histoire Naturelle, France
MOM, Museé Oceanographique du Monaco, Monaco
NMSZ - National Museums of Scotland, Natural History, UK
ROM - Royal Ontario Museum, Department of Ichthyology and Herpetology, Canada

SIO - Scripps Institution of Oceanography, Marine Vertebrates Collection, USA
UF - University of Florida, Natural History Museum, USA
USNM - Smithsonian Institution, National Museum of Natural History, USA
YPM - Yale University, Peabody Museum of Natural History, USA
ZIN - Zoological Institute of the Russian Academy of Sciences, Russia
ZMH/ ISH - University of Hamburg, Zoologisches Museum, Germany
ZMMU - Zoological Museum of the Moscow State University, Russia
ZMUB - University of Bergen, Museum of Zoology, Norway
ZMUC - University of Copenhagen, Zoological Museum, Denmark

Sampling gears

EMT 1400 - Engel Midwater Trawl
EMT 1600 - Engel Midwater Trawl
EMT 80-630 - Engel Midwater Trawl -
IKMT 10’ - Isaac-Kidd Midwater Trawl
IKMT 10’ DDS - Isaac-Kidd Midwater Trawl
IKMT 6’ - Isaacs-Kidd Midwater Trawl
IYGPT 100 - International Young Gadoid Pelagic Trawl
MOCNESS 10 (MOC 10; MOC 10 N1) - Multi Opening/ Closing Net and Environmental Sensing System (10 m^2)
MOCNESS 20 (MOC 20; MOC 20 N1) - Multi Opening/ Closing Net and Environmental Sensing System (20 m^2)
NN - Neuston net
R1.5m - Ring net 1.5m
R1m - Ring net 1m
R2m - Ring net 2m
R3m - Ring net 3m
RMT 10 - Rectangular Midwater Trawl
RMT 50 - Rectangular Midwater Trawl
RMT 8 - Rectangular Midwater Trawl
RMT 8 MC - Rectangular Midwater Trawl (opening-closing system)

TT 5 - Tucker trawl
YFT 100 - Young Fish Trawl

bt - bottom trawls
mwt - unspecified midwater trawls
c_mwt - commercial midwater trawls
m_mwt - micronekton midwater trawls
m_mwt_o - non-closing micronekton midwater trawls
m_mwt_oc - open-closing micronekton midwater trawls
p_mwt - plankton midwater trawls
nn - neuston trawl

Chapter 1 - General Introduction

Large-scale classification of marine ecosystems – The Oceanic realm

The classification of marine ecosystems in the sea into coherent units is as arbitrary as it is for any ecosystem of the Planet. The divisions depend of the scale one considers, and the objectives of the study.

A general geographical division of the sea is based on the positions of the water masses relative to the continents. The division of the World Ocean into Atlantic, Pacific, Indian, Artic and Southern Ocean has been universally accepted. Then, the ocean basins can be divided into south and north and at a lower hierarchical scale, into seas, basins, gulfs, bays, etc. Islands and seamounts are grouped into archipelagos and clusters of archipelagos. Distinct topographic features, such as mid-ocean-ridges, can also be considered to be natural boundaries.

At a global scale, another general partitioning is between oceanic and neritic waters. The frontier between these two regions is usually delimited by the shelf break, where the continental margin gives way to the slope. Along most continental margins the shelf break approximately coincides with the 200m isobath; the most conspicuous exception being around Antarctica where the weight of the ice shelf has depressed the shelf break to a depth of ~500m. However, around oceanic islands and seamounts the boundary between these two realms is generally indistinct, whereas along the continental margins the division of oceanic and neritic environments is most conspicuous.

Other divisions can be based on the distribution of water masses, and on the general circulation patterns associated with them. The physical processes underlying these entities and dynamics are linked to global climatological processes. The equilibria in this dynamic environment change over timescales ranging from small, to meso (e.g. North Atlantic Oscillation) and then to geological scales. The hydrology is forced by atmospheric circulation and thermohaline mechanisms, especially those associated with heat fluxes. Water masses have characteristic chemo-physical proprieties determined predominantly at the sea-surface and so respond in a predictable way to seasonal fluctuations, which play a major role on the control and expression of biological processes.

Ecological subdivisions of the seas compartmentalize the oceans into regions, with relatively consistent environmental and biological properties. The terms, tropical, sub-tropical, temperate or boreal, polar etc., derived from terrestrial biogeography are generally applied.

Classically biogeographers have subdivided the oceanic realm according to recurrent distribution patterns of organisms, which are believed to be linked with physical proprieties of the seas. A plethora of concepts and associated terminology have been created when trying to rationalize the various theories, as a result, biogeographic sub-divisions of the ocean are almost as numerous as the authors that described them.

Another approach to ecological classification subdivides the marine environment according to bathymetry and dependence on the sea floor. Thus the terms benthic, benthopelagic and pelagic have arisen and are often recognised (in large-scale studies) as large biotopes.

Classifications of oceanic environments based on bathymetric features are also largely accepted for neritic and oceanic waters. These classifications can be based on physical or chemical features, such as the photosynthetic compensation depth, which is determined by light penetration, the depth of the pycnocline, thermocline and/or halocline, the occurrence of nutriclines, oxyclines or in deeper water the depths of the carbonate compensation depth and the lysocline. Alternatively they can be based on biological characteristics of the communities that inhabit these strata. For the water column, the expressions epipelagic, mesopelagic, bathypelagic, abyssopelagic, and hadalpelagic, relate to increasing depths of the water column from surface down to the abysses and ocean trenches. The water overlying the seabed (to a height of ~100m) appearing to be a special zone often referred to ecologically as the benthopelagic and physically as the benthic boundary layer. Controversies persist about the precise definitions and position of the boundaries of these bathymetric zones, but their existence is largely recognised.

Other boundaries are political; in some cases the political boundaries coincide with ecological boundaries, but many political borders are environmentally arbitrary and are aimed at the assessment and management of the natural resources (fish stocks, oil, etc.) and/or of the quality of the environmental and/or its conservation.(e.g. the FAO [Food and Agriculture Organisation of the United Nations] and ICES [International Council for the Exploration of the Seas] statistical areas, and the OSPAR [Convention for the Protection of the Marine Environment of the North-East Atlantic) regions).

This thesis will focus on the techniques used to sample the pelagic realm, and how best to use the resulting data to study the biogeography and diversity of Stomiidae midwater fish in the North Atlantic Ocean. The total geographical area considered is delimited by the equator, to the south, and by the Artic Ocean, to the north. It includes the Mediterranean Sea, the Caribbean Sea, the Gulf of Mexico, and the northern part of the Gulf of Guinea. The fish are distributed throughout the region. All species are oceanic and most are pelagic. Some species regularly ascend into the epipelagic layers at night, whereas others have broad bathymetric ranges that extend down to depths of ca. 5000m. However, the bathymetric centres of distribution of these fishes are predominantly in the meso-bathypelagic region.

Pelagic biogeography/biodiversity

The general aim of biogeography is to describe the geographical distribution of living things and relate these patterns to environmental and evolutionary processes over all time-space scales. This is a massive undertaking, and only now is it emerging how large and complex the task actually is. Comprehensive knowledge of past distribution patterns will probably never be achieved, although palaeosciences do shed some light on the evolution and extinction of organisms and on the dynamics of past pelagic communities through studies of the fossil record. The oceanic biome is in essence undescribable, because of the inherent limitations of observational methods, the high degree of natural variability at all scales, and our inability to integrate and model all this complexity. However, this seemingly insoluble puzzle is progressively being clarified at rates never previously experienced.

The definitions of biogeography are numerous, as are the theories that endeavour to explain them. However, as pointed out by Marshall (1979) there is only one global biogeography, as life evolved and is part of the same Natural History.

Descriptions of terrestrial biogeography are much more advanced than those of the marine environment. For obvious reasons, marine science captured the imagination of the scientific community later and evolved slower. Within the marine sphere, open ocean pelagic biogeography has received relatively little attention.

The present concept of biodiversity was formalised about twenty years ago and incorporated all the biological variability from genes to ecosystems. For operational proposes, the term was defined as "the total diversity and variability of living things and of systems of which they are part" (Heywood and Baste, 1995). This eclectic concept encompasses and integrates the knowledge gained from genetics, physiology, ecology, evolutionary biology, palaeontology, taxonomy, phylogeny, systematics and conservation. Biogeography is also considered to be an important component in understanding biodiversity. Indeed, several authors when approaching subjects traditionally included as part of the biogeography now refer to them under "pelagic biodiversity" (e.g. Angel, 1997). Biodiversity should be understood as a broad unifying concept similar to natural history. However, a more manageable interpretation of biodiversity is to relate it to species taxonomic, morphological and ecological diversity. The role played by diversity in the functioning and evolution of oceanic ecosystems is a poorly investigated subject.

Nevertheless, biogeography, as a multidisciplinary branch of the biological sciences is well defined and recently the ecological branch of pelagic biogeography evolved to a technologically driven science (see Longhurst, 1998b).

Steps toward the actual pelagic biogeography science

Interest in pelagic oceanography arose during the last decades of the 19th century. Pelagic biogeography evolved slowly through the early decades of the 20th century. During the 1930's the broad distributional ranges of some of the commoner deep-sea pelagic species, especially fishes, were thought to be well described (e.g. Ege, 1934; Bruun, 1936). The bulk of the data used by the authors were collected from the geographically extensive DANA expeditions. However, it was only after Sverdrup et al. (1942) that a new conceptual framework for understanding pelagic biogeography emerged: the 'water masses' hypothesis. Several studies related distribution data of pelagic fauna with water masses, superimposing distribution data on the temperature-salinity diagrams. Large pelagic (epi- and mesopelagic) surveys, promoted by Americans, Russians, British and Germans, among others, were being undertaken in most of the major ocean basins. An ecologically driven pelagic biogeography was evolving. The role of the evolutionary history on pelagic biogeography was recognised as being crucial, recognising the implications of plate-tectonic theory.

Empirical global patterns of species distributions were delineated; currents, water masses, convergence and divergence zones, temperature, oxygen, productivity, stability of mixed layer, were environmental factors that were considered to affect species distribution. The significance of biotic-biotic and biotic-environment interactions were (as they still are) seldom recognised.

McGowan (1971, 1974) and Reid et al. (1978) were influential papers towards an integrated ecological perspective of pelagic ecosystems. Pacific communities were linked to water masses and their properties. Following similar concepts Backus et al. (1977) subjectively arranged the complex Atlantic mesopelagial into a comprehensive biogeographic system based on Myctophidae distributions. Beklemishev et al. (1977) in a key paper classified the pelagic biota distribution in a hydrological context; the concepts of cyclical (gyral), peripheral, transitional, distant-neritic, terminal, etc., waters and faunas were introduced. Parin (1984) summarised the main findings of the Russian school as applied to oceanic fishes. Many of the patterns described were broadly coherent but a high degree of variability was apparent. Haury et al. (1978) introduced the concept of space - time variability to pelagic ecosystems. Although this theme was incorporated into the science, it had minor practical application.

Van der Spoel and Pierrot-Bults (1979) edited a series of reviews on pelagic biogeography and diversity. Among other relevant contributions, Angel (1979) presented a historical, physical and ecological description of the Atlantic. The conceptual framework of pelagic biogeography evolved further with Van der Spoel and Heyman (1983) atlas of global distribution patterns of selected pelagic species. A new biogeographic synoptic areal subdivision of the world ocean was drawn based on biotic distributions (summarised from several sources), hydrology and distribution of physical and chemical seawater properties. Most of the data were for pelagic holoplankton. A direct relationship between (micronekton) mesopelagic distribution patterns and those found at the upper layers was assumed. Van der Spoel and Heyman (1983) was the first to apply cladistic methods to historical analysis of pelagic biogeography.

The First International Conference of Pelagic Biogeography (Pierrot-Bults et al., 1986) demonstrated the contemporary vitality of the science. A multi-disciplinary group produced forty-five papers describing old and new theoretical and methodological approaches. Among them: McGowan (1986) and Backus (1986) summarised the main “paradigms” of the ecological school of pelagic biogeography; the fractal dimension of the pelagic realm (time-space scales) was visited by Haury (1986); Haedrich (1986) analysed the size spectra of a mesopelagic Myctophidae fish communities; specificities of benthopelagic fishes were noted (Merrett, 1986); the pelagic species concept (Gibbs, 1986e) and polytypy (Johnson, 1986) were discussed. The need for applied genetics studies was recognised as crucial (Marcus, 1986). Van der Spoel (1986) postulated that population dynamics and evolution rather than water masses are responsible for the equilibria of contemporary patterns of distribution. This theory was further developed (van der Spoel, 1994b).

The SCOR Working Group 93 produced a series of reviews and incorporated new concerns about pelagic systems, namely biodiversity and anthropogenic impacts (among other relevant subjects). Van der Spoel (1994a,b) introduced new and discussed old concepts in pelagic biogeography. Boundaries, species ranges and speciation, pelagic ecosystems, communities, populations, biotope, habitat, niche and patches; these were approached in the context of the uniqueness of the pelagic realm. A new concept emerged that primary and secondary related-communities, ecotones and nodal point of stress, are governed by the stable-biotope and/or substrate-biotope conditions; species and assemblages can respond both in a deterministic or adaptive ways to habitat change and variations. Olson and Hood (1994) assessed and applied mathematical models to pelagic biogeography (dispersal through dynamic physical boundaries), stressing the models' utility in depicting the complexity required to explain biogeographic patterns.

The perception that science should be addressing public concern and awareness of the impacts of anthropogenic effects in natural systems motivated the papers from Omori et al. (1994), van der Spoel (1994c) and Krause and Angel (1994). The first consistent cladistic approach on evolutionary pelagic biogeography (of the Pacific) was published (White, 1994).

The second Pelagic Biogeography Conference (ICoPB II, 1995) was similarly productive for pelagic biogeography at which fifty papers were presented (Pierrot-Bults and van der Spoel, 1998). The progression of the science was evident and new analytical tools were applied. The results of many ecological (on seasonal dynamic of holoplankton, vertical distribution, trophodynamics) and biogeographic (distribution of plankton through vast regions) studies were presented. Speciation, species morphological and genetics variability, were emergent themes discussed. Cladistics supported some studies on historical biogeography. Several contributions developed biological-physical mathematical models applied to plankton dynamic. Space-time scales and fractal analysis were revisited. Climatic changes and plankton distribution, and effects of anthropogenic activities were discussed. New technologies to support future research were presented. Longhurst (1998a; following Longhurst, 1995) was a seminal contribution presented at this conference. The biogeochemical partitioning that influences productivity cycles and seasonality in the Global Ocean was detailed later (Longhurst, 1998b; see Appendix 1.1).

The conclusions of the ICoPB II, 1995 were summarised by Pierrot-Bults (1998a). She reported that pelagic biogeography needed input from biological and ecological studies, meso-scale biogeographic insights into expatriation and the functioning of boundaries; genetics (genetics diversity, speciation; gene flow; etc.; phylogeny); and historical biogeography (palaeoceanography; hydrotectonics; cladistics). Improvements in sampling methodologies were needed together with an increase in the sophistication of observational programs incorporating new technologies and the development of mathematical models to develop and test hypotheses requires high quality data in readily available electronic form. She stressed the high potential of the existing biological collections and databases that are currently underused, for biogeographic studies, and highlighted the need of metadata about those resources. Central key words for the future work were: monitoring; network of stations; indicator species; long-term time series; modes of variability; global changes; anthropogenic impacts; societal awareness; data integration at time-space scales; modelling and predictions.

Studies on North Atlantic midwater fishes biogeography/biodiversity

The early approaches

The early reports dealing with meso- and bathypelagic fish only outlined the geographical distribution of some of most abundant species. The DANA Expeditions, to the North Atlantic (1920-22) and around the World (1928-1930), were the most significant early initiatives promoting mesopelagic biogeography, even considering all the technological limitations of the sampling programs. The contribution of Ege (1934), on systematics and distribution of *Stomias* species was pioneering. Distribution patterns were related to water temperature, and the geographical replacement of one species by another was demonstrated. Co-occurring species were considered to be segregated by depth, although the sampling regime using open nets provided little depth discrimination. *S. colubrinus* was reported to maintain disjunct populations in the eastern tropical Atlantic and Pacific. North Atlantic occurrences were more detailed than elsewhere.

Bruun (1936) produced a more conceptual note about pelagic biogeography. External (environmental) and internal (physiological) factors were considered to control the distribution of marine organisms. Temperature was considered to be the main factor constraining the distribution of species; salinity, oxygen and food availability (productivity), while important, were thought to be secondary factors. Disjunct populations restricted to subtropical gyres of Atlantic, Indian and Pacific were mapped and contrasted with the circumpolar distributions of equatorial faunas. Bi-subtropical (bitropical) disjunct populations living in the northern and southern gyres were reported, as other distributional patterns of temperate and boreal species. Distributions of Anguilliformes (mainly larvae), myctophids, paralepidids and *Stomias* were all described. Later, Bruun, (1958) published a note referring to the peculiarities of Pacific and Atlantic eastern tropical faunas. It was suggested that eastern tropical *Stomias* (at that time considered a unique species with disjunct distribution) was sustaining its restricted distributions by adjusting its life history (namely ontogenetic vertical behaviour) according to the dynamics of the equatorial undercurrent.

Bolin (1959) treating the bipolarity of the oceanic fishes, speculated about the emergence of disjunct North Atlantic populations of species (or groups) which had originated in the Indo-Pacific (Myctophidae). The author hypothesised a pathway of dispersion ("involuntary migrations") around the southern tip of Africa via the Agulhas Current, and the subsequent transport of individuals northwards via the Benguela Current and Equatorial current system. Temperature of equatorial waters was viewed as a limiting factor for larvae survival. In the subtropical North Atlantic adult stragglers reached a suitable niche in which they were able to live and reproduce successfully.

The water masses hypothesis

Pickford (1946; for the deep-sea cephalopod *Vampyroteuthis infernalis*) and Haffner (1952) published the precursor papers of modern ecological pelagic biogeography. The second author benefited from the systematics work done by Ege (1948; on *Chauliodus*) and using DANA material compared the geographical and vertical distribution of related taxa with the hydrography. Stimulated by the advances achieved by Sverdrup et al. (1942), Haffner used temperature-salinity (T-S) diagrams to match the distributions of fish populations into envelopes of T-S. Allopatric distributions among *Chauliodus* species and sub-species were depicted. *C. schmidti*, a tropical eastern Atlantic species, was considered to be adapted to a low-oxygen environment.

Ebeling (1962) produced a classic work linking the systematics of midwater fishes (genus *Melamphaes*) with pelagic biogeography. The water masses hypothesis was developed; T-S curves of captures (of the water column at the haul position) were plotted in T-S diagrams of water masses. Species were considered to be fitting their distributional ranges to a water mass, and this was recognised to be a rule. The author reported, however, the complexity of the system and depicted productivity as another key factor affecting the actual distribution patterns. Centres of origin, dispersion paths, ontogenetic distribution, expatriation, gene flow, isolation, adaptation and allopatric speciation were discussed in detail. Geological events were at that time considered important in shaping the present faunistic patterns. Ebeling (1962) compiled information on the distributions of many Pacific midwater fishes species (13 families and 135 species) and created a hierarchical system of global pelagic biogeographic regions, relating physical oceanography with the observed distribution patterns. He identified six major patterns: central, equatorial, central-tropical, transitional, boreal, and antitropical. Boundaries delimited faunal regions and water masses. In Ebeling's four level hierarchical system the North Atlantic (as the other oceans) was divided into primary regions (Mediterranean; Atlantic Subarctic and Circum-central tropical), secondary regions (Atlantic central split from Circum-central tropical region) and tertiary regions (Western North Atlantic central; Eastern North Atlantic central; and Atlantic tropical). The author predicted that plankton would also match this biogeographic system.

Ebeling and Weed (1963) found a more confused picture when studying *Scopelogadus* species. Vertical distribution patterns were found to confuse the relationships between species and water masses. Based on morphological differences, the authors discussed speciation and geographical distribution of bathy- and mesopelagic species.

Later, Ebeling (1967) substantiated his theory by reviewing new data on species distributions patterns and physical/biological oceanography. He focussed more attention on the importance of areas of enhanced productivity (convergence zones and upwelling regions), and identified several transitional regions (ecotones) with a mixed of faunas from adjacent gyral systems. He was also amongst the first to identify multivariate statistics as important analytical tools.

Baird (1971) discussed distribution patterns of Sternoptychidae species, adopting the water masses hypothesis. Using these hatchfish species distributions as a surrogate and the described water masses discontinuities, the author created another scheme of mesopelagic zoogeographic regions. In the North Atlantic nine zoogeographic regions were identified: Tropical, Venezuelan-Caribbean; Caribbean-Gulf Central; Gulf Peripheral; NW Atlantic Pocket; Western North Atlantic Central; Eastern North Atlantic Central; NE Atlantic Subarctic; and Mediterranean. The definition of these regions, by fitting distribution patterns to water masses, was somehow confused by the presence of many species in the majority of the regions.

The Institute für Seefischerei (ISH) contributions

Several ocean-scale midwater transects conducted by the ISH took place during late 1960's and 1970's (see Post, 1987). Krefft (1974, 1976) studied the distributions of Atlantic meso- and bathypelagic fishes caught during those surveys. A large commercial trawl (the Engel MT 1600) was used to sample the large-bodied pelagic fauna that had seldom been caught previously by the conventional micronekton gears. Krefft (1974) described thirteen non-quantitative distributional patterns organised at a three level hierarchical system: northern temperate (divided in boreal and temperate-subtropical); sub-tropical (biantitropical; intrageneric bipolarity; and restricted to one gyre); tropical (broadly tropical [divided in several sub-patterns related with productivity regimes] and strict tropical [split in broad equatorial, eastern and western equatorial]); pseudoceanic (and other restricted patterns); and bipolar (at both temperate hemispheres). He reported bathypelagic patterns; these fishes were considered to have a broader distribution patterns. A bathy- benthopelagic fauna was recognised. Krefft (1976) improved the patterns previously defined. Novel biogeographic data on deep-mesopelagic and bathypelagic fishes at the eastern North Atlantic, South Atlantic and Southern Ocean were presented. The existence of feeding grounds and spawning grounds for large midwater inhabitants (e.g. *Anotopterus*, *Lampris*, *Trachypterus*, etc) were detected at north and south of the Polar Front, respectively. An impoverished Boreoarctic fauna was identified, and the influence of the Polar Front emphasized. The fauna of the Southern Ocean received much attention and several previously described distributional patterns were re-evaluated. A review of the distribution patterns of alepocephaloid fish detected a fauna associated with eastern Atlantic islands and South Atlantic Mid-Atlantic-Ridge. The later feature was recognised as being an effective east-west barrier for several species of the bathy- benthopelagic fauna (thalassobathyal). Hulley (1981) gave continuity to biogeographic approaches based on ISH material. He reviewed the systematics of Myctophidae and speculated about the physical parameters that may constrain the species distributions. He constructed a hierarchical scheme of zones (high-oceanic and pseudo-oceanic), communities, groups, patterns and sub-patterns to fit the observed species' distributional ranges. The patterns and sub-patterns were described based on oceanographic properties and species composition. They were compared with the distributional patterns defined by Backus et al. (1977; see below). Later Hulley and Krefft (1985) used multivariate techniques (cluster and Multi-Dimensional Scaling to evaluate the accuracy of the North Atlantic subtropical boundaries of Backus et al. (1977).

The Atlantic Pelagic Zoogeography

Backus et al. (1977) created a classical biogeographic system that sub-divides the Atlantic Ocean (to 30ºS) into 6 faunal regions and 19 provinces, based on data from seventy-five species of Myctophidae, which were fitted into nine distributional patterns. This is, to date, the most synoptic study on the biogeography of the Atlantic mesopelagic fish, and according the authors it could prove to be of general application to pelagic biota. It represented the culmination of a long series of surveys (ca. 20 cruises) carried out by the Woods Hole Oceanographic Institution (WHOI) between 1961 and 1974. Backus et al. (1977) was based on the detailed taxonomic and distributional account on Atlantic Myctophidae, presented in the same volume (Nafpaktitis et al., 1977). Besides the presence and absence of individual species, the distribution maps presented in the latter paper gave indications of species abundance. The same authors had published several other papers previously as preliminary outputs of the Atlantic Pelagic Zoogeography program (Backus et al., 1965 1969, 1970). Backus and Craddock (1977) reported the cruise data that underpinned the system. The sampling strategy adopted for those biogeographic surveys was aimed at maximizing the catches, rather than systematically sampling the full water column. The sampling was conducted mainly within the dense shallow Deep Scattering Layer (DSL) during the night (from surface to 200m), and in the upper and middle mesopelagial during the day (<600m). The sampling rational was presented by Backus, et al. (1965, 1969, 1970). The technique was established principally to depict faunal boundaries along transects (Backus et al., 1965), but proved problematic. The analytical method defined the horizontal boundaries of the provinces by matching faunal changes (of a "constituency of species") with *a priori* recognised physical features of the large-scale ocean circulation. The method is not obvious and the authors recognised its inadequacy. Johnson (1982) reviewed this system and pointed to some pertinent methodological and conceptual inconsistencies. Examples given are the primacy of physical oceanographic features to depict the provinces' boundaries and the loss of the ability to recognise faunas; the ranges of individual species normally extended far beyond the geographic area and/or the faunal pattern to which they were assigned. Nevertheless, the author concluded that Backus's system is a powerful tool and discussed the distribution of North Atlantic Evermannellidae and Scopelachidae in relation to the biogeographic system and the distribution patterns defined by Backus et al. (1977). Many other authors have used the system as a framework into which they have fitted the distributional patterns of their pelagic organisms.

Later, Backus (1986) reaffirmed his conviction that faunal boundaries are consistent with the "water masses hypothesis", but the author did not clarify whether the regions and provinces do indeed hold consistent and identifiable faunal assemblages. Haedrich (1986), using the material of Backus et al. (1977), analysed the biomass size spectra of myctophids. He was able to show differences in fractal dimension and size spectra between provinces of the system.

The global distribution of Evermannellidae and Scopelarchidae

Johnson (1974, 1982) reviewed the systematics of the meso- bathypelagic fishes of the families Evermannellidae and Scopelarchidae. In 1982 he reviewed biogeographic theories and concepts, and evaluated their implications for the pelagic realm. He criticized the simplifications proposed by several approaches, namely those on "water masses hypothesis" and those that focus strictly on centres-of-origin versus dispersal. Relevant papers on distribution and biogeography of micronekton organisms were assessed. Evermannellidae and Scopelarchidae were classified according to a hierarchical system of distribution patterns of four levels. Inshore/offshore, cold-water/warm water, ocean basin, and water mass region were the primary divisions. As the families studied live essentially within the warm-water-sphere, patterns for that region were extensively discussed. Patterns included: species restricted to a water mass; and species more widely spread. The last group was divided into: Subtropical (Biantitropical or restricted to one gyre); Tropical or Equatorial; Tropical-Subtropical in 3 basins. Johnson (1982) mentioned that no “generalized-tracks” were found (with the available data) but agreed that a limited number of patterns could accommodate most of the distributional configurations. The patterns were comparable to those of Krefft (1974) and Backus et al. (1970, 1977). However, the paucity of Evermannellidae and Scopelarchidae species in the North Atlantic, compared to Indo-Pacific, and the absence of endemics (and boreal fauna), limited the discussion about this basin. The highly consistent data, both oceanographic and biological, from the Eastern Tropical Pacific supported a detailed approach for that region. An evolutionary history of the warm water species assemblages (as a unit of evolution) was hypothesized. A preliminary cladistic (phylogenetic) approach using scopelarchids illustrated Johnson’s historical speculations. The author argued, however, that (at that time) no phylogenetic studies were available to support a proper insight into an ecological/historical zoogeography.

The midwater fish fauna of the Northeast Atlantic

In contrast to the studies of Backus and Krefft and co-workers who adopted a sampling strategy to depict Atlantic biogeographic patterns (among other subjects), the former Institute of Oceanographic Sciences (IOS, UK) targeted meso- and small scales features of midwater communities (see Angel [1977] for differences in sampling strategies). The used of an efficient multi-closing gear (the Rectangular Midwater Trawl) and the standardization of sampling procedures provided detailed insights into the vertical structure and faunal gradients in the North-eastern Atlantic. Badcock and Merrett (1977) compared the vertical distribution of selected midwater fishes caught at six stations located along a meridional section (11º-60ºN, 20ºW). The authors differentiated swimbladdered from swimbladderless species and compared the relative distribution, and behaviour, of those groups. Latitudinal changes in species composition and vertical behaviour (namely for *Cyclothone* spp, *Argyropelecus* spp and *Benthosema*) were presented. Pelagic boundaries were detected at ca. 18ºN and 40ºN, affecting diversity and relative abundance of mesopelagic fish fauna. Light and temperature gradients, and biotic relationships (e.g. interspecific competition), were viewed as important factors influencing the patterns observed. The results were interpreted with caveats because of the intrinsic variability of behavioural patterns, lack of seasonal approach, and selectivity of the gear used. Stratification of species by size, sex and maturity was found to constrain the interpretation of vertical patterns and the correlations with environmental factors.

The Soviet contributions

Several institutions from the former USSR investigated in detail the midwater fish fauna of some North Atlantic regions. Soviet biologists adopted primarily the biogeographic concepts developed by Beklemishev et al. (1977). Kukuev et al. (2000) summarised the biogeography of midwater fish fauna of the northern section of Mid-Atlantic-Ridge and Northeast Atlantic. Based on material collected by several fisheries-related surveys (both targeting larvae and adults), the authors depicted four distribution patterns: Boreal-Subarctic, Boreal, Boreal-subtropical (peripheral) and Tropical-subtropical (widely-tropical). The distributions of micronekton fish (termed as macroplankton) were explained in terms of the prevailing hydrology. The picture drawn is of an ecotonal fauna associated with a transient (or transitional) region. Autochthonous and allochthonous elements were distinguished mainly based on the relative abundance of larvae. Widely-tropical (i.e. tropical-subtropical) species were considered to be advected by the North Atlantic Current and viewed as ecological marginal in the ichthyocoenoses. However, the existence of an “unsterile drift zone” that accommodates viable widely-tropical species was considered and three species were assigned to it.

Many other contributions have produced relevant information about the fish fauna living in the North Atlantic pelagial (e.g. Kashkin, 1982a,b, 1988; Boltachev, 1994; Kukev, 2002; Kukuev and Trunov, 2002).

Evolutionary pelagic biogeography approaches

The historical biogeographic approach of Gibbs (1969) reviewed the genus *Stomias* and defined its phylogeny (based on meristics) by arranging the species into groups of different evolutionary ages. Tectonic events (i.e. the closure of Tethys Sea) and historical climatological changes (i.e. the glacial periods of Pleistocene) created the isolation that allowed speciation. According to the author, the most derived (and abundant) species occupy complementary ranges in the more productive waters of the world. Existing primitive taxa were subsequently excluded or displaced by competition to peripheral, often specialized, environments. Rarity and/or restricted geographical distribution of older species was interpreted as an effect of that competitive exclusion. The study was a good exercise but the currently accepted phylogeny of *Stomias* is somewhat different (Fink and Fink, 1986).

White, (1994) presented the first consistent historical (cladistic) approach to pelagic biogeography. His analysis comprised the following steps: production of an area-cladogram of Pacific surface waters (based on hydrotectonic vicariance); recognition of faunistic “generalised tracks”; revision of influences of productivity regimes on distribution; definition of phylogenetic predictions; analysis of dispersal (e.g. related with the oxygen minimum layer) and extinction; and the overlay of the area-cladogram on the phylogeny of monophyletic pelagic fish genera (*Evermannella* and *Stomias*; from Johnson [1982] and Fink and Fink [1986], respectively). Relationships between faunal assemblages (defined in terms of species composition) were interpreted in the light of water masses history. The author concluded, “that some ancestral biogeographic patterns have persisted into the present day”. He claimed phylogenetic studies at species level to be an indispensable requirement to test hydrotectonic hypotheses. The existence of allopatric taxa was pointed also as an important aspect for the applicability of the method.

Johnson and Zahuranec (1998) emphasized the scarcity of phylogenetic studies at species level as the main limitation for historical pelagic biogeography studies. The paper summarizes the contributions made to historical biogeography using midwater fish species, and presents a new approach. Several *a priori* postulates were essential for the exercise: the recognition of old and stable central water masses; the neritic origin of midwater fauna; and the ultimate occupancy of stressful systems (i.e. older taxa dwell first in more “benign” productive and stable equatorial and peripheral tropical sub-tropical regions); central gyral endemic faunas are the most derivatives members of monophyletic groups. Following these assumptions the “ecocladograms” generated for Scopelarchidae, Evermannellidae and *Stomias*, were show to be phylogenetically rooted in warm-water regions. Species from cold waters were classified in terminal nodes in the phyletic cladograms. However, the method could not be applied successfully to the myctophid genus *Nannobrachium* (see also Zahuranec, 2000). Criticisms of White’s

(1994) approach were: 1) the limitation of White's study to Pacific Ocean, which only allowed the discussion of one branch of the whole tree; and 2) the lack of resolution in the area-cladogram concerning the warm-water masses, considered to be the centre of origin of those faunas. To illustrate the lack of knowledge regarding this subject Moi and Gill (2002) in a recent review about historical biogeography of fishes do not give any information about deep-sea pelagic species.

Systematics and geographical data

Distributional data often turn up in papers on taxonomy of a specific taxon. The numbers of contributions dealing with the systematics of North Atlantic mesopelagic fish is immense. A review of those treating Stomiidae is presented in Chapter 5. Often new systematics revisions conflict with the biogeographic conclusions derived under the previous systematics framework. The specific taxonomic status of many midwater fishes (as for other pelagic organisms) remains unstable, even for groups previously thought to be well know (e.g. Parin and Kobyliansky, [1996] for *Maurolicus* and Zahuranec [2000] for *Nannobrachium*, a new myctophid genus created from *Lampanyctus*). Moreover, the actual concept of biological species varies according taxon and author's criteria; in mesopelagic fish, species-groups are often proposed to include highly similar species (e.g. Gibbs et al., 1983; Gibbs, 1986; and Chapter 5).

In another perspective, the ecological concept of populations (as of communities) is considered to be problematic when applied to pelagic organisms (van der Spoel, 1994b). Several authors have studied polytypy in midwater fishes (e.g. Johnson and Barnett, 1972, 1975; Badcock, 1981; Johnson, 1986; Badcock and Araújo, 1988; Gartner, 1998) and wide ranging morphological variation seems to be the rule. A general difficulty is to recognize whether the observed variation either reflects plastic responses to ecological regimes (i.e. ecophenotypes), or if it indeed represents infra-specific genetic diversity (i.e. genotypes adapted to different abiotic and/or biotic factors). Disjunct populations are expected eventually to show genetic divergence related with the duration of isolation (e.g. following a vicariant event); whereas species with a continuous pattern of distribution are expected to show a clinal diversity variation, depending of gene-flow rates. The use of molecular techniques to solve these questions is of crucial importance.

Phylogeny of monophyletic groups

As mentioned, the lack of studies on species phylogeny is the major constraint to study the evolutionary history of pelagic groups. Furthermore, the disagreement between the results obtained (i.e. the relationships between species) by studies using different methodologies also compromises the approach. This can be highlighted by the phylogenetic research on Gonostomatidae by Harold (1998) and Miya and Nishida (2000). The first author carried out a cladistic analysis based on morphology, whereas the latter authors undertook mitochondrial DNA sequencing. The conclusions drawn by a historical biogeographic investigation of Gonostomatidae will be dependent on which of these studies is selected. Moreover, the presence of any cryptic species may lead to erroneous conclusions. Molecular phylogenetic studies on *Cyclothone*, *Sternoptyx* and *Gonostoma* have been published by Miya and Nishida (1996, 1998, 2000, respectively).

Genetic diversity in mesopelagic fishes

Miya and Nishida (1997) studied the genetic structure of the wide spread species *Cyclothone alba*. They identified five morphologically identical sister populations that have undergone independent evolution and have “attained reciprocal monophyletic status with low level of gene flow”. However, close genetic relationships were not always reflected in contiguous zoogeographical ranges or patterns that are consistent with known vicariant events. Western North Atlantic samples showed higher affinity with those from the Central North Pacific! Samples from the Western North Pacific population were more closely related with those from the Equatorial Indian Ocean, than to those from the Western South Pacific! There was some relationship between genetic diversity observed and vicariant events (as the closure of the Tethys Sea and of the Indo-Pacific channels), but other within-ocean fragmentation appears to have occurred without any discernible barriers. The work implied the existence of cryptic genetic diversity, as described for *Gonostoma ebelingi* of Hawaii and Coral Sea (Miya and Nishida, 2000), in which there are two demographic units that are morphologically similar but genetically distinct. Probably, the genetic diversity of midwater fish (as for other pelagic organisms) may well prove to be higher than actually recognised. However, genetics studies on population structure of mesopelagic fish populations have been neglected. Apart from the studies by Miya and Nishida few other reports could be found in published literature (e.g. Suneetha et al. [1999], for genetic substructure of *Benthosema glaciale* in different fjords and Norwegian Sea).

Data relevant to a biogeographic approach of the North Atlantic mesopelagial

The DANA Expeditions (Schmidt, 1929; Anonymous, 1934; Tåning, 1944), the WHOI study (Backus and Craddock, 1977) and the ISH initiative (Post, 1987), generated the bulk of the data used herein to study the biogeography of midwater fish in the North Atlantic. However, there is no doubt that studies on regional faunas provide relevant biogeographic information.

Northwest Atlantic (Slope Water, Gulf Stream and Sargasso Sea)

The mesopelagic fauna of northwestern North Atlantic is amongst the most thoroughly studied. The Labrador Sea, the Slope Sea, the Gulf Stream and the Sargasso Sea have received considerable attention since the study of Goode and Bean (1896). However, during the recent decades the sampling programs targeting the mesopelagic ichthyofauna have intensified.

Jahn and Backus (1976) contributed to the pelagic zoogeography study by Backus et al. (1977) and was aimed at identifying differences between fish faunas of Northern Sargasso Sea, Gulf Stream and Slope Water, using multivariate analysis. The faunas were discriminated in terms of their biomass, diversity and species composition. McKelvie (1985a) criticized this work mainly because the Labrador Current was not considered (a region expected to contribute to the overall pool of species). McKelvie sampled the Newfoundland basin and adjacent regions and found no clear relationship between water masses and the faunas: whereas individual species respond to the environmental variability, no assemblage does. Using multivariate (ordination) techniques it was concluded that changes in faunal composition at the northern Slope Water are gradual rather than abrupt, and hence form an ecotone. An extrapolation for a general clinal distribution of pelagic organisms, as apposed to discrete patterns was hypothesised.

D. Themelis and R. Halliday (Themelis, 1996) extensively sampled the Slope Sea epi- and upper mesopelagic layers (see ARC entry in Appendix B). Themelis studied the species composition of the mesopelagic fish assemblages, their vertical structure, dynamics, spatial and seasonal variability. He found a region of high species richness, where there was a significant number of rare species (63%), thought to have been expatriated via the Gulf Stream system. Most of common and abundant species were recognised as having been advected in; only six widespread and temperate species were found to be self-sustaining in the warm Slope Water and no endemics were found. The Gulf Stream was observed to be a leaky boundary for North Sargasso Sea fauna. Discontinuities, within the regions, were detected by abrupt shifts of biomass but not in the presence/absence data. With this background scenario the author identified a persistent Slope Water fauna, showing a certain degree of predictability and shaped by extrinsic factors. The community identified was viewed as structured on stochastic processes of mixing and advection of water and fauna.

Other contributions inventoried the midwater fauna sampled in the Slope Water (Scott and Scott, 1988; Musick, 1973; McKelvie, 1985b; McKelvie and Haedrich, 1985). Kukuev (2002) summarises the results of a latitudinal transect across the Gulf Stream in discuss the species occurrences in a biogeographic context.

Recently Moore et al. (2003a) compiled an exhaustive list of the deep-sea fishes (pelagic, benthic and benthopelagic species) of the New England region (Slope Water). The authors reviewed the published data and studied the material deposited in the main American ichthyological collections holding samples of deep-sea fish from that region (e.g. MCZ, YPM and USNM; see Appendix D).

Gulf Stream mesoscale eddies (rings)

Eddy fields occur throughout most of the ocean and have a relevant role on the large-scale circulation patterns. Eddies (or rings) are mesoscale transient structures that induce local instability and transfer parcels of water (and energy, salt, nutrients, contaminants, etc.) and biota over long distances. Eddies contribute greatly to the mesoscale variability on the faunal assemblages, promoting dispersal, expatriation, patchiness and aggregation of organisms. They contribute to the maintenance of wide genetic variability by facilitating gene-flow but they play a role on reducing speciation (see Angel, 1997). The best-studied eddy fields are those associated with the Gulf Stream. Warm- and cold- core rings (WCR and CCR) impact considerably the ecology of Slope Water and Northern Sargasso Sea, respectively. The WHOI carried out two multidisciplinary programs aimed to study both CCR and WCR (Ring Group, 1981; Craddock et al., 1987). Backus and Craddock (1982) studied the mesopelagic fishes of both sides of the Gulf Stream and those associated with CCR. Craddock et al. (1987, 1992) described quantitatively the vertical dynamics and the transport of Sargasso Sea midwater fish fauna into the Slope Water by WCR. Haedrich (1972) and Olson and Backus (1985) are other contributions on the effects of Gulf Stream rings on mesopelagic fish distribution and dynamics.

Bermuda and Sargasso Sea

The midwater fish fauna of Bermuda is probably the most thoroughly studied in the North Atlantic. The area has been investigated by a series of large-scale oceanographic expeditions and by vessels from the main East coast US oceanographic institutions, throughout the 20th century. Beebe (e.g. 1932b, 1937) sampled offshore of Nonsuch Island over more than two years and made about 1500 net-hauls. The area was intensively surveyed by Backus and co-workers (see above). However, the major contribution has come from the Bermuda Ocean Acre Program (OA; Gibbs and Krueger, 1987; Gibbs and Karnella, 1987; 1967-1972, 14 cruises, 1175 hauls, 45% discrete). Species composition, vertical migration and structure by size and sexes, patchiness, reproduction, feeding ecology, and niche partitioning, integrated in a seasonal basis, have been presented for several fish families of midwater species (Myctophidae, Sternoptychidae and Melamphaidae), but not for Stomiidae (see Gibbs and Krueger, 1987). The conclusions of publications and the technical reports produced under the Ocean Acre program are listed by Brooks and Saenger (1991).

Antilles, Caribbean Sea and the Gulf of Mexico

The Antilles, Caribbean Sea and the Gulf of Mexico harbour a highly diverse mesopelagic fauna and attracted many of the early expeditions. Many of the DANA reports deal with the systematics of fish caught at that area (e.g. Regan and Trewavas, 1930). Bekker et al. (1975) listed 165 mesopelagic fish caught at Caribbean Sea and Gulf of Mexico. They observed that the overall composition of the fauna was homogeneous throughout the area, but is patchily distributed. Biogeographically, the assemblage was characterized by a mix of species that elsewhere occupy distinct distributional patterns (e.g. neritic distant, northern central, broadly tropical and equatorial). Murdy et al. (1983) also produced faunal lists for the area. Gartner et al. (1987) and Sutton and Hopkins (1996a) presented specific composition, biogeographic data, relative abundance and vertical distribution of Myctophidae and Stomiidae of the Gulf of Mexico. McEachram and Fechhelm (1998) compiled an exhaustive list (with morphological descriptions and keys) of the fish of the Gulf of Mexico.

Northeast Atlantic

Information on the mesopelagic fish of the Northeast Atlantic are scattered throughout the literature. Whitehead et al. (FNAM; 1984-86) have provided the main synthesis of that knowledge. The IOS made a huge sampling effort inside the area, but comprehensive faunal lists from those surveys are unavailable. The authors concentrated on the vertical dynamics of the community as a whole (e.g. Roe et al., 1984). Badcock (1970), Roe (1974), Badcock and Merrett (1976, 1977) and Roe and Badcock (1984) analysed the mesopelagic fish caught. The material is preserved at the Natural History Museum, London.

Post (1988) published on mesopelagic fishes caught off the British Isles, reporting species composition, relative abundances, and approximate vertical distributions of the assemblage. The occurrences of many (Stomiidae) species previously unrecorded from the area were reported. Swinney et al. (1986) reported on the results of a research conducted in the Gulf of Biscay that was aimed at evaluating the influence of lights mounted on the net on the catchability of midwater fish. An extensive list of the fish caught is provided but accurate station data are lacking. This paper also details some observations reported on earlier by Clarke and Pascoe (1985) off Madeira. A general conclusion was that hauls with nets carrying lights caught more and larger fish, during both day and night.

Central North Atlantic

The Central North Atlantic, around the Azores, was intensively surveyed by the Prince of Monaco (Richard, 1934). However, the gears employed failed to sample efficiently midwater fishes. The relatively few specimens collected were mainly analysed by taxonomists. The region lay along on the tracks of many large-scale expeditions so the fauna has been sampled regularly (Porteiro et al., 1999). Santos et al. (1997) produced an annotated checklist of the fishes from the area. Domanski (1986) presented a preliminary analysis of the fish caught at the vicinity of the Azores Front. Kashkin (1988) studied a collection of mesopelagic fish caught in the central Atlantic to the south west of the Canaries (North Equatorial Current). He summarised the species composition, relative abundance and the biogeographic structure of the assemblage. The species recorded were a mix belonging to eight recognised distributional patterns.

Tropical Northeast Atlantic

The mesopelagial off the Canary Islands has been sampled by many expeditions that crossed the archipelago. However, the SOND cruise (Foxton, 1969) was the first intensive survey (with a sampler using a catch dividing cod-end) made in this region. The multidisciplinary program produces several scientific papers and showed the complexity of a pelagic community (see Badcock and Merrett [1976] for a summary). Badcock (1970) listed the fish fauna caught during that expedition and analysed the vertical distribution of the most abundant species. The area was revisited later and new contributions were published. Badcock and Merrett (1976) examined the fish catch composition and refined the analysis on vertical distribution structure. Later, the patterns observed were compared with those at other stations to the north and south along 20ºW (Badcock and Merrett, 1977). Rudyakov (1979a,b) re-analysed the data from the SOND cruise to detailed patterns in the dynamics of vertical migration.

Recently, a program targeting ecological relationships between epi- and mesopelagic fishes took place around the Canaries Islands (Bordes et al., 1999, 2000; Wienerroither, 2001, 2003), and produced relevant information about the mesopelagic fish fauna of the region. An exhaustive catalogue of the littoral and oceanic fishes of Canaries has been published (Brito et al., 2002).

Several large-scale (and a few mesoscale) oceanographic programs sampled the midwater fauna of the eastern tropical Atlantic (Krefft, 1966; Kotthaus, 1972; Backus and Craddock, 1977; Post, 1987). However, few of those papers reported details of the catches. CLOFETA (Quéro et al., 1990) exhaustively inventories the fish fauna (and related references) of the region.

Off Northwest Africa a particular fauna occurs in the upwelling region. There is a blend of elements with different geographic affinities: equatorial, tropical, sub-tropical, Mediterranean, subpolar-temperate and temperate. Some species probably occur there as disjunct populations. Backus et al. (1977) recognised the Mauritanian Upwelling Region, but Badcock (1981) characterized the mesopelagic fish fauna (especially Myctophidae) living there better. Based on infra-specific meristic variations and distribution (vertical, geographical and onslope/offslope) of *Benthosema glaciale*, both adults and larvae, Badcock (1981) discussed in detail the "pseudocenic" populations in the upwelling niche. However, the relationships between the population inhabiting the upwelling zone and that living in the Mediterranean could not be discriminated. Badcock highlighted the need to investigate other pelagic taxa, to elucidate the relationships between the faunas of the temperate North-Eastern Atlantic, Mediterranean, Canary Current, and Upwelling areas.

Mediterranean

The Mediterranean Sea was surveyed extensively during the first decades of the 20th century by the Danish Expeditions. It was observed to have an impoverished deep-sea pelagic fish fauna relative to that of the adjacent Atlantic waters and with few or no endemics. The fauna contains elements that show marked affinities with both the Northwest Africa Upwelling community and with the northern temperate regions. Goodyear et al. (1972) detailed the vertical structure and dynamics of the mesopelagic fish fauna caught during an west-east transect along the basin. Fredj and Maurin (1987) summarised the ichthyological data from a database of Mediterranean fauna (MEDIFAUNE). During the last glaciation just 25my ago, the Mediterranean and the adjacent Atlantic environments were very different, and the exchange of species through the Strait of Gibraltar would have been dramatically different, hence the presence of 'glacial relicts' there (e.g. *Bethosema glaciale*, *Borostomias antarcticus* and the euphausiid *Meganyciphanes norvegica*) that are living in atypical environmental conditions.

Polar seas

The mesopelagic fish fauna of Reykjanes Ridge and the Irminger Sea was intensively survey by the Marine Research Institute, Iceland, in order to assess and manage the pelagic commercial fisheries of redfish. The composition and dynamic of the deep scattering layers was presented by Magnusson (1996) and by Sigurðsson et al. (2002).

Distribution maps of relative abundance of species per depth strata were presented by the latter authors.

North Atlantic benthopelagial

Soviet and Russian institutions implemented exploratory surveys targeted at assessing fishery resources of slopes, rises, seamounts and ridges. Trawlling expeditions fished a benthopelagic fauna that included, among others, large individuals of species usually thought meso- and bathypelagic. Parin and Golovan (1976), Golovan (1978) and Parin et al. (1978) produced lists of the ichthyofauna associated with the continental slope off West Africa. Taxonomic notes, cruise data and a discussion on the structure of the ichthyocoenose, are given. Many stations were carried out at the eastern South Atlantic, outside the area considered in this study. Further north, Kukuev (1982) inventoried the pelagic and the thalassobathyal fishes caught by fisheries surveys over the Corner and the New England Seamounts. Vinnichenko (1997) published a list of fish species caught in the Corner Rising Seamount region (1976-96), but no cruise data are given. The biogeographic approach of Kukuev et al. (2000) on Mid-Atlantic-Ridge and European slope ichthyofaunas was primarily based on papers published previously (Gushchin and Kukuev [1981] and references therein), which targeted mainly that biotope. New data comparing the benthopelagic faunas of several seamounts complexes in the North Atlantic were published by Kukuev (2004).

Several other studies reported benthopelagic species belonging to families thought to inhabit the meso- and bathypelagic layers (e.g. Uyeno et al., 1983; Merrett, 1986; Alpoim et al., 2002). Moore et al. (2001, 2002, 2003b) analysed the composition and the diversity of the fauna (invertebrates, fish and mammals) caught at the Bear Seamount (the westernmost seamount of the New England Seamounts Chain).

Comprehensive data on regional and global faunas

Regional inventories

The volumes that make up the Fishes of the Western North Atlantic (FWNA), published by the Sears Foundation for Marine Research, provide authoritative references for surveys of midwater fishes from the Atlantic. The study considers the systematics and related subjects of hundreds of species, organised by families. Backus et al. (1977) is one of these contributions. Several species have undergone a considerable taxonomic revision since then but these improvements can be tracked using for example FishBase.

Another pertinent contribution is the three volumes of Fish of the North-east Atlantic and Mediterranean (FNAM; Whitehead et al., 1984-86). In these books each chapter considered a family, giving with taxonomic keys for the genera and species known to occur in the area (from 30ºN to Arctic and to 30ºW). Each species entry includes morphological, ecological, behavioural and geographical data, summarised by the most experienced ichthyologists. The FNAM followed the Checklist of Fish of the North-east Atlantic (CLOFNAM; Hureau and Monod, 1973) where synonyms and references were given for the species. A CLOFNAM number links the species dealt with in the two publications.

Following a layout similar to that of CLOFNAM, the Check-list of the Fishes of the Eastern Tropical Atlantic (CLOFETA; Quéro et al., 1990) is the taxonomic authority for fish species known from the region. In addition to the data on type material data, synonyms, references and systematics notes, brief accounts of the geographical distributions, maximum sizes, and vertical distributions are provided.

The increasing demand for biodiversity data has stimulated many concerted international initiatives to inventory regional faunas and floras. The European Register of Marine Species (ERMS; Costello, 2000; Costello et al., 2001) is amongst the most authoritative of these programmes. An inventory of species (the common currency of biodiversity) is viewed as the starting point for research and management of marine biodiversity. The regional list is considered basic to establish systematics (nomenclature) uniformity; to evaluate the relative diversity of higher taxa; to contribute information on species distributions; and to summarise the existing knowledge and to identify gaps in knowledge and highlight priorities to further investigations. The ERMS links with other large-scale or global electronic databases such as the Species 2000 (www.sp2000.org) and the UNESCO-IOC Register of Marine Species, and others. The ERMS network of scientists will be continued through BIOMARE (an EU marine biodiversity concerted action). The program aimed to improve the databases and include additional information on species distribution.

The FishBase – a global ichthyological database

FishBase (Froeser and Pauly, 2000; www.fishbase.org) is the most promising contribution for a comprehensive worldwide inventory of ichthyofauna. The potential of this database is enormous in all fields of the ichthyology. This initiative stimulates the compilation of the information available, by reviewing published material (including grey literature), by integrating ichthyological collections catalogues, and by the direct inputs from members of the international scientific community. The work is evolving rapidly and according the authors this electronic facility can also be use as a research tool that allow modelling (namely Ecopath models) and testing of scientific hypothesis. Up to now, the data concerning midwater fishes have not been completely assessed, but the paucity of information on this group of fishes reflects a real lack of knowledge.

The Eschmeyer (1998) Catalogue of Fishes, published by the California Academy of Sciences, supported the systematics adopted by the FishBase. This is considered the ultimately authoritative reference concerning the genera and species of fishes. Higher taxa follow the classification presented by Nelson (1994).

Census of Marine Life (CoML)

This global initiative aims to explain the diversity, distribution and abundance of marine life in a global context. The Alfred P. Sloan Foundation launched this titanic international action (see Grassle and Stocks, 1999; Grassle, 2000) and promotes international networking and field studies to give substance to the initiative. Ausubel (1999) summarised the results of the first CoML workshops, detailed in a special volume of Oceanography (12 [3/1999]). Several pilot-studies are being implemented under the umbrella of the CoML. The Ocean Biogeographic Information System (OBIS) (Grassle, 2000; http://www.iobis.org) and the MAR-ECO (Bergstad and Godø, 2003; www.mar-eco.no) are important initiatives that are contributing for the understanding of open ocean pelagic ecosystems.

Ichthyological collections

Natural History Museums and other collections facilities constitute the major repositories of global biodiversity. The recognition of the value of those collections for biodiversity/biogeographic studies is widely accepted today (Pierrot-Bults, 1998a;

Grassle, 2000; Paterson et al., 2000). For many decades voucher specimens have been used primarily by taxonomists. However, the increase interest in biodiversity issues has stimulated the use of these collections to study distribution patterns of organisms at several scales. The material is widely dispersed in collections all over the world and the assessment of the species they contain was a very difficult task before the Internet Age. Many institutions (mainly in the USA) have electronic versions of their paper catalogues that make available a significant amount of data for the global community. Nevertheless, large quantities of data (e.g. from European collections) are only accessible from the traditional paper catalogues. However, this scenario is changing and some initiatives may encourage the general implementation of electronic catalogues (e.g. FishBase, Froeser and Pauly [2000]; FISHNET, OBIS and other CoML projects; Vieglais et al. [2000]).

It is claimed that collections provide valuable services, namely to hold reference (type) material, set the standards for describing diversity, and help in the definition of methodologies and strategies for future sampling programs.

Leviton et al. (1985), Kottelat et al. (1993) and Poss and Collette (1995) compiled metadata about ichthyological collections in America and Europe, respectively. Their papers provide information about the extent of the collection, habitat represented, geographical areas covered, published catalogues, type material etc., and a standard acronym for each of the institutions assessed.

Objectives of this work

1. To review concepts, methodologies and field programmes used to approach the biogeography/biodiversity of North Atlantic midwater fish fauna;
2. To evaluate and compile data on North Atlantic midwater programs (through occurrences of Stomiidae) existing in ichthyological collections (mainly Natural History Museums); to produce metadata about those collections;
3. To compare sampling strategies and the relative effectiveness of fishing devices used to sample the North Atlantic Stomiidae midwater fauna;
4. To survey the actual status of the Stomiidae systematics;
5. To evaluate the global biogeographic patterns of the North Atlantic Stomiidae assemblage; to delineate species distribution ranges and summarise the observed

variability through distribution patterns; to evaluate the usefulness of Longhurst's (1998b) eco-geographic system to approach the basin-scale distribution of Stomiidae;

6. To characterise the biodiversity of Stomiidae assemblages associated with North Atlantic Longhurst's provinces; species composition, spatial trends and gradients;
7. To discuss the usefulness of Stomiidae as a surrogate for North Atlantic midwater biogeography/biodiversity.

Chapter 2 - General Material and Methods

Data sources

This study is based on data from ichthyological collections (Natural History Museums and other), reported in selected bibliography, and obtained by recent midwater surveys (Fig. 2.1a). The area under study extends from the equator to about 70ºN and from 100ºW to 35ºE, at the latitudes of Gulf of Mexico and Mediterranean.

Ichthyological collections

The majority of the records included in the Stomiidae database are reported from European and North American ichthyological collections (Appendix B).

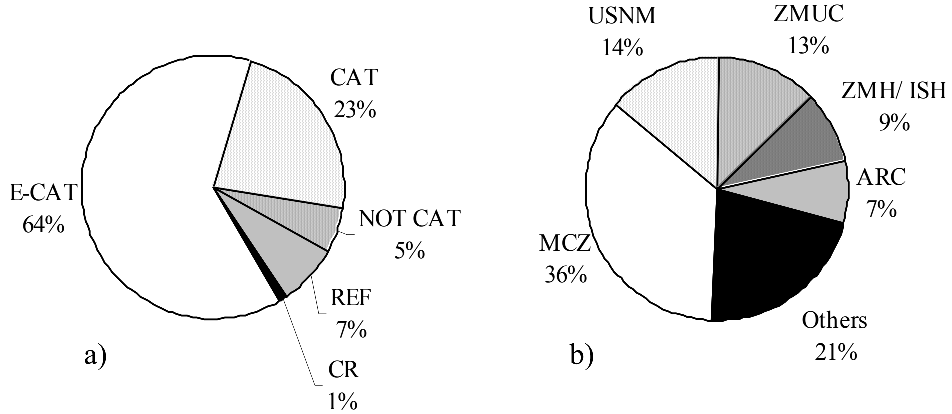


Figure 2.1 Sources of the data incorporated in the Stomiidae database (S_db). a) records from ichthyological collections with electronic catalogues (e-cat); with paper catalogues (cat); and preserved but not catalogued (not cat); records from bibliography (ref); and records from surveys (cr). b) holdings (percentage) of the most important ichthyological collections (for acronyms see Appendix B or List of Acronyms).

The most relevant collections holding North Atlantic midwater fishes were visited and their stomiids critically reviewed. The identification of Stomiidae taxa from sorted and unsorted material was completed. In total about 1000 additional records not reported in catalogues were retrieved. Data from institutions with no electronic catalogues were entered as reported in their paper catalogues. Information about the non-surveyed collections was downloaded either from e-catalogues accessible at the institutions web sites, or received from the institutions, or scanned from selected references on stomiid occurrences.

Appendix B shows metadata for the most representative source collections. Five collections are responsible for more than two-thirds of the Stomiidae entries (Fig. 2.1b). Nevertheless, the Natural History Museum, London (not shown in that figure), holds much more material than that reported here (see BMNH entry in Appendix B).

Selected references

The detailed information from the Russians ichthyological collections was inaccessible. The data from Russian research were obtained from the following contributions: Novikova, 1967; Parin and Pokhilskaya, 1974, 1978; Parin and Novikova, 1976; Shcherbachev and Novikova, 1976; Parin and Borodulina, 1996, 1997b; Kashkin, 1982; Bekker et al., 1975; Gushchin and Kukuev, 1981; Kukuyev, 1982; Parin and Golovan, 1976; and Parin, et al., 1978. Those papers referred to species systematics, ecology, faunal lists and many are associated with benthopelagic samples. The full set of 415 Russian records accounted for 2.1% of the total. The entries provided useful information on species distributions, but their value is reduced by the low quality of the cruise data associated with the records.

Several institutions (e.g. Institute of Oceanology of the Academy of Sciences, IORAS; Zoological Museum of the Moscow State University, ZMMGU; Zoological Institute of the Academy of Sciences, ZIN; etc.) hold more mesopelagic material from the North Atlantic (Appendix B). A small-scale program (under the scope of MESOPE; see Acknowledgments) translated selected Russian papers (translated in Literature Cited).

The systematics work carried out at the Smithsonian Institute (USNM) also supplied additional entries (mainly Goodyear, 1980; but also, Morrow and Gibbs, 1964; Gibbs et al., 1983; Gibbs and Amaoka, 1984; see Chapter 5).

The records made by the Prince Albert I of Monaco expeditions were compiled from Zugmayer (1911a,b), Roule (1919), Vaillant (1919) and Roule and Angel (1933). The material, including several types, is deposited either at Musée Océanographique du Monaco (MOM) or at the Museé National d'Histoire Naturelle (MNHN).

Koefoed (1956) reported on the fish caught by the North Atlantic Deep-Sea Expedition, 1910.

Additional information from the Canaries Basin was obtained from Kotthaus (1972; distributional data) and from Bordes et al. (1999; the Canaries material preserved at ZMUC was only partially used).

Surveys to the Azores Region seamounts

Between 1994 and 2000, the DOP/ UAC carried out several small-scale field programs around the Azores Islands targeting the mesopelagic fauna (Table 2.1). Moreover, I participated in one cruise to Mid-Atlantic Ridge Seamounts (HE -135) led by the Alfred Wegener Institute (C. Pusch, AWI, German; Pusch et al., 2002). C. Pusch kindly provided data from a cruise to the Meteor Seamount (METEOR-98-42-3). The records obtained by these programs represent about 1% (ca. 200 records) of the total data incorporated in the *S_db*.

The Stomiidae database

A database was designed to accommodate the compiled data (Appendix C). The Stomiidae database (*S_db*) assembles positive records of Stomiidae by species. The data includes: taxonomic, morphological, ecological and geographical information about North Atlantic stomiids, linked to and supported by cruise and gear data (sampling data).

Cruise data validation and standardization

Only a few collection catalogues have high quality cruise and biological data associated with their records. To improve this information the databases were checked, corrected and filled-in by checking the original data against published cruise data. The account on ichthyological collections (Appendix B) and the accounts on selected gear (Appendix D) give relevant references used to update the *S_bd*. Papers dealing with the material are of two kinds: 1) those specifically dealing with Stomiidae systematics, which focus on selected taxonomic groups (see Chapter 5); and 2) those that deal with the distribution or ecology of midwater fish assemblages. The first set normally report occurrences compiled from several collections; whereas the second set deals with data from specific individual cruises.

Cross referencing the catalogues

Participants from several institutions (e.g. USNM, ZMUC, ISH and BMNH) often shared data from the catches of the cruises, in which they participated. Such sharing has

Table 2.1 Summary of cruises made by the R/V *Arquipélago* (IMAR/DOP- UAç) and R/V *Heicke* (HE 135; AWI, Bremenhaven) to the Mid Atlantic Ridge seamounts in the Azores Region.

HE 135

Local: Gulf of Biscay; Twins seamount; Atlantis seamount; Azores; Gulf of Biscay
Vessel: Heicke (Alfred Wegener Institute, Bremenhaven, German)
Gears: Young fish trawl, BONGO nets, CTD
No. of tows: 103
Depth: 0-900 m
Date: 24.07.2000 – 21.08.2000

ASIMOV

Local: Bank D. João de Castro (38º 12-15’ N 026º 32-36’ W)
Depth: 0-200m
No. of tows: 4
Date: 21.08.99 – 02.09.99

FCA 97 (C1/2)

Local: Azores Front-Current (31-33º N 029-031º W)
Depth: 0-300m
No. of tows: 8
Date: 19.07.97 - 04.08.97

ARICTIO I

Local: Princes Alice Bank (37º 49-50’N 031º 29-31’W)
Gears: RMT 8, BONGO nets
No. of tows: 41
Depth: 0-600 m
Date: 07.10.99 - 12.07.99

CRISTA1

Local: Menez Gwen (37º 49-50’N 031º 29-31’W) and Lucky Strike (37º 17-18’N 032º 16-17’W)
Depth: 0-220m
No. of tows: 5
Date: 24.06.97 - 01.07.97

FCA 94

Local: Azores Front-Current (31-33º N 029-031º W)
Depth: 0-200m
No. of tows: 3
Date: July 1994

introduced noise into the original databases, as specimens of the same species from the same net-haul have been entered as two separate records, since they occurred in more than one collection. So these records have been merged, although this has lead to assigning two or three catalogue numbers to a single record. Also, within the same museum, specimens belonging to the same species and collected during the same net-haul have been catalogued in separate lots. Those data have been corrected, but again the records have acquired multiple catalogue numbers.

Cross referencing records within and between collections has not only enhanced accuracy and standardization but has allowed the reconstruction of cruise series.

Filling the gaps

Geographical position. Only geo-referenced data has been entered into the database. Some net-hauls did not originally have geographical data (i.e. latitude and longitude) but were associated with identifiable topological information (e.g. ca. 170 km SE off Nova Scotia; SE of Madeira Island; 125 miles southeast of City Hall, New York City; Off Puerto Rico). Using standard charts and atlases it was possible to assign acceptably accurate geographical coordinates (to within one degree) to those records (this was necessary in <0.5% of the total net-hauls.

Some data sources give a station number but not all the relevant station data; the exact location of each net-haul is not reported but the station at which the sampling was conducted was carried centred around a fixed position (e.g. 30ºN, 23º W for Badcock and Merrett, 1976) or confined within multi-station areal boxes (e.g. Gushchin and Kukuyev, 1981; Kukuev, 1982). In these cases the coordinates reported (or the central position within a box) were accepted. Those records have in general very low quality cruise data.

It might also be worth noting that until satellite navigation became generally used (sometime during the 1980's), the precision of navigation could be low. This was the case during prolonged periods of cloudy weather when sun or star sights were impossible for several days. Moreover, dead reckoning errors could accumulate in regions of strong currents or where there was high mesoscale activity. Also the Americans built in errors in the algorithms during the Cold War so 'hostile' states could not rely on the system for precise positioning!

Time fishing. It is the operation time from launch to recovery if fishing with open nets. In several data sets this information was absent or represented a different time interval. For example, the Department of Fisheries and Oceans (DFO) cruises off Canada (see ARC in appendix 2.1) had no time of fishing. However, Themelis (1996) reported a standard 30 min haul for both gears employed (International Young Gadoid Pelagic

Trawl and Tucker Trawl 5; see IYGPT 100 and TT 5 in Appendix D) while fishing at depth (infrequent exceptions were also noted). In relation to ISH surveys (see ZMH/ ISH in Appendix B), time fishing available from Post (1987) also relates to the time which lapsed while fishing at depth (horizontal tows). In these situations the time fishing assembled is the time reported plus the time needed to achieve the maximum depth plus that required for recovering the net. This is equivalent to time needed to perform an oblique tow. The relationship between paying out and hauling the net to a certain depth was calculated from hauls made during "Heincke"-135 cruise (Table 2.1), which used a Young Fish Trawl, a net similar to that used by the DFO. The length (x) - weight (y) relationship was better explained by a linear function ($y = 3E\text{-}05x + 0.0016$; $R^2 = 0.897$), indicating that the operation to launch and pay out the net are slower for shallower hauls.

Cruise data from the R/V "Challenger" 83-14 cruise (National Museums of Scotland, Natural History, NMSZ; G. Swinney) also had no fishing time available. Clarke and Pascoe (1985) reported for that program a standard haul of two hours fishing at depth; the time from launch to recovery of a RMT 50 was calculated using the rate of paying out and hauling of 50 m/ min, as noted by the authors.

Night and Day. If time data indicate the day-hours instead of standard haul length, it was possible to link a haul to light or dark conditions. However, to assign dusk and dawn to hauls is not so easy as it varies with geographical position and season. The web site of the U.S. Naval Observatory (http://aa.usno.navy.mil/dta/docs/RS_OneDay.html) provides a universal sunset and sunrise schedule that was used to assess in several situations. However, it is worth noting that different ships work on different times (i.e. some adjust their clocks according to longitude whereas others work to a specific time zone - e.g. Greenwich Mean Time) and that in the past the 'time' used was not consistent, nor was it necessarily logged. Most of the computer based navigational systems universally used at sea now used GMT.

Depth. The database has two fields related with depth: the maximum depth reached by a net during a tow, wherever the trawling strategy adopted (i.e. horizontal, oblique or step hauls); and the minimum depth, which is zero (surface) for every non-closing device.

Earlier reports (as some recent ones) provided fishing depth in metres of wire paid out (mwo). Despite the high variability of the relationship between the amount of wire paid out and sampling depth (because mainly of differential currents between surface and towing depth) a relationship was obtained from several sources (e.g. Backus and Hersey [1956] and Foxton [1969] for the IKMT 10); from Stomiidae_db records, with both mwo and depth reached; and data from the HE-135. On average, a ratio of 2.5 between mwo and maximum depth was assumed. However, the value applied might underestimate the true sampling depth of the hauls performed by the array of ring nets used during the “DANA” expeditions.

It can be accepted that many inaccurate data still persist because many of the early depth pressure gauges (as those used by Backus and Foxton) suffered from hystersis (i.e. they gave a different depth going down to coming up and the differences could be as great as 50m in 1000m). Moreover, the Americans tended to tow their IKMTs at 2.5 to 3 knots whereas Foxton towed his at 2 knots (~1ms^{-1}) and then the mwo as a measure of depth could be in error by up to 50%!

In several North American collections depth is expressed in fathoms instead of metres, a universal metre scale was used.

Gear. Many different gears sampled the North Atlantic midwater micronektonic fauna. The data were assembled, standardized and classified. Gear data diversity and procedures to handling that are presented in chapter 3, where gear performances are analysed.

Sampling strategy. Three basic sampling strategies were identified: horizontal hauls (the net is lowered, trawled at depth and hauled to the surface); oblique hauls (the net is lowered and, reaching depth, towed to surface); and step-hauls (when the net is trawled discontinuously at different depth layers). Different institutions in different periods normally adopted different standard sampling strategies. Variability observed was high and data on sampling strategy were not systematically compiled.

Species systematics

A detailed survey on Stomiidae systematics is a primary requirement for a study on biogeography and biodiversity. In many of the collections visited the systematics of the stomiid lots were evaluated. Many of them were identified, re-identified, checked and updated relative to current synonyms. Fortunately, R.H. Gibbs and his team (associated with USNM and other institutions) systematically studied large numbers of fish in every collection available and they used that material to support the profuse systematics accounts they produced. The actual systematics of North Atlantic Stomiidae species (and synonymization), detailed in chapter 4, is quite stable. Most data on the type material of North Atlantic Stomiidae were assembled from collections catalogues. Some, however, were entered from bibliography because they are in collections that just hold type material collected during historical surveys that target the midwater fauna.

Biological data

Specimens size range (SL). Only a few collection catalogues report on a regular basis, sizes of their fish (e.g. the MCZ collection). An important proportion of the fish size data used herein was obtained from measurements done in the collections. This accounted for more than 5000 specimens measured. Size data were also compiled both from papers on stomiid systematics (chapter 4) and from species lists of mesopelagic fish caught during a specific survey (e.g. Grey, 1955; Koefoed, 1956; Badcock, 1970; Bekker et al, 1975; among many other cited throughout the text). The sizes of *Stomias* spp. and *Chauliodus* spp. caught by the Danish expeditions were compiled from Ege (1918, 1934, 1948) who categorized the specimens into several size classes; the same classes were entered.

Number of specimens. Despite all the effort to compile information on fish numbers and size, some records still included no numerical data. In these cases it was assumed each lot contained at least one fish. Some entries have combined catalogue numbers, which indicate the number of fish in that lot (i.e. P208725-27 = 3 specimens). This rule was confirmed in more than 40% of the ZMUC lots.

Geographical classification

The eco-geographic system of Longhurst (1995, 1998a,b) was adopted as the biogeographic framework of this study. A summary of that system is provided in Appendix A. In practical terms it partitions the oceans hierarchically in biomes and provinces. The North Atlantic encompasses four biomes that embrace 12 oceanic and 5 coastal provinces (see Fig. 2.2a for geographical boundaries, acronyms and full names). This arrangement was used as a factor to group data: statistical biogeographic areas (see Chapters 6 and 7).

Net-hauls (= *field_codes*) were assigned to a regular grid of 5º per 5º latitude/longitude squares (*sq_5x5*) that covers the North Atlantic basin. The grid extends from west of Greenland (at 70ºN) south to Gulf of Guinea, comprising a total of 218 grid squares (Fig. 2.2b), and allows for pooling data per each *sq_5x5*. Each pixel was allocated to one of Longhurst's biomes and provinces.

Data manipulation

Relationships between weight and length

Stomiid species weight-size data were obtained from cruises "Challenger" 14-83 and "Heincke"135, 2000. The numbers allowed computations of the weight (W) - length (L) power relationships ($W = aL^b$) for 50 species and 18 genera. The species were categorised into five groups according the parameters of the equation. Morphometric relationships (such as the body depth body length ratio) enabled the remaining species, for which no weight-length data were available, to be attributed to one of the five groups established. In the end it was possible to estimate the biomass of the stomiids caught by every net-haul incorporated in *S_bd*. However, one underlying assumption of this method is that every stomiid fish caught by a net-haul has been recorded in the database.

Catching abilities of trawls

The analyses assembled net-hauls by gears and by Longhurst's provinces. The sampling unit considered was the net-haul (*field_code*). The number of species and the number and size of specimens were used to characterize the catch of each sampling unit. Intra-gear comparisons allowed for computations of a standard-haul for each gear (only for those regularly used). Standard-hauls were compared and calibrated based on their relative ability to catch stomiid fishes. Gear standardization permitted the fishing effort of each haul to be calculated within a given region. Detailed procedures are presented in Chapter 4.

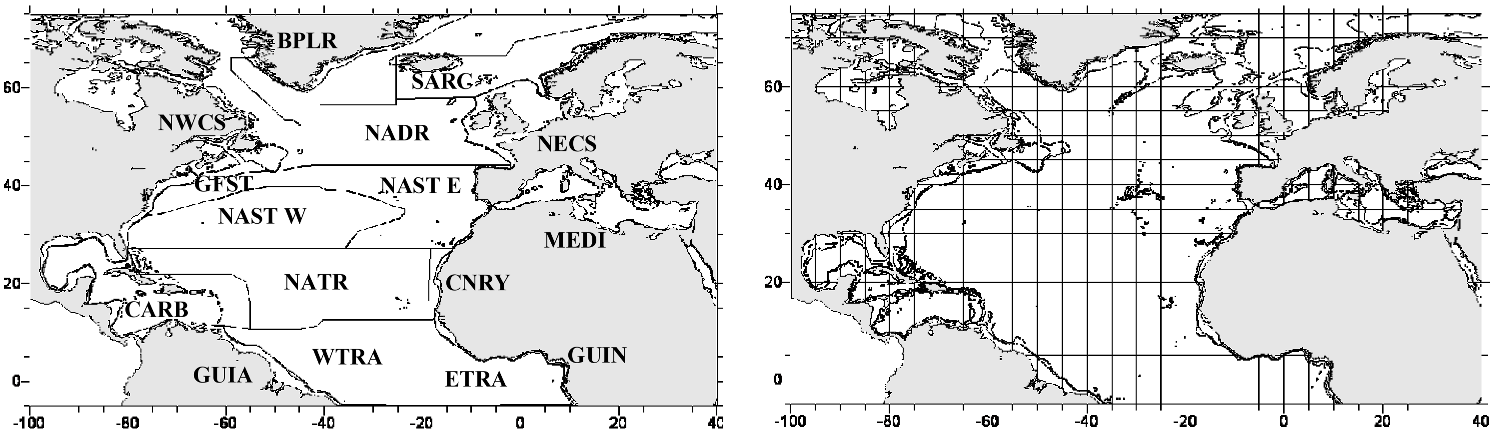


Figure 2.2 a) Ecological Geography of the Sea (Longhurst, 1995, 1998a,b): North Atlantic Biomes and Provinces; b) North Atlantic 5º per 5º latitude, longitude grid (*sq_5x5*).

Trade Wind Biome (**ATWB**): Eastern Tropical Atlantic (**ETRA); ** Western Tropical Atlantic (**WTRA**); North Atlantic Tropical Gyral (**NATR**); and Caribbean (**CARB**).

Westerly Winds Biome (**AWWB**): North Atlantic Subtropical Gyral West and East (**NAST W**; **NAST E**); Gulf Stream (**GFST**); North Atlantic Drift (**NADR**); and Mediterranean (**MEDI**).

Polar Biome (**APB**): Atlantic Subarctic (**SARC); ** Atlantic Arctic (**ARCT); ** and Boreal Polar (**BPLR**).

Coastal Biome (**ACB**): Guinean Current (**GUIN**); Guianas (**GUIA**); Canaries (**CNRY**); Northeast Atlantic shelves (**NECS**); Northwest Atlantic shelves (**NWCS**).

Biogeography

Having a measure of the relative standard fishing effort for each gear, which was comparable to all other gears, it was possible to estimate the fishing effort made per unit area (*Lgh_P* or *sq_5x5*). Then by dividing the captures from an area by the catching effort it was possible to obtain relative abundances of each species throughout its range of distribution. Species were fitted in distributional patterns and their geographical distributions were described in relation to the hydrology of the North Atlantic. The effects of Longhurst's fuzzy boundaries on the observed patterns are discussed. Multivariate analysis elucidated the relationships between faunas from the Longhurst's provinces (the regional pool of species).

Biodiversity

Analyses of biodiversity (species richness and dominance) patterns of North Atlantic stomiid used the spatial reference systems described (i.e. the grid of 5x5 latitude/ longitude squares and the Longhurst's eco-biogeographic system). The approach is based on a series of dominance curves (i.e. rarefaction, abundance and geometric curves) and on a battery of standard and new biodiversity indices (Chapter 7). Species richness, dominance and evenness were compared across natural gradients produced by biogeographic provinces. Species assemblages and discriminator species were obtained for each province. Spatial distribution of biodiversity indices and a comparative analysis between regional (provincial) and local (averaged *sq_5x5*) biodiversity was performed.
Multivariate analysis, using biodiversity indices, contrasted the biodiversity of the different Longhurst's provinces. Kriging was used to produce the spatial distribution of some biodiversity indices.

Statistics

Univariate non-parametric and parametric testes were used to compare means and variables distribution. Multivariated statistiscs (Cluster Analysis, Principal Components Analysis, Multidimensional Scaling) supported several studies. Most of the procedures followed the techniques described by Field et al. (1982) and Clarke and Warwick (1994) and implemented in the ecological package PRIMER v5.5.2 (Clarke and Gorley, 2001). Geostatistical analysis (kriging) was used to interpolate biodiversity data distribution.

Surfer 7.0 was the mapping software used to produce the maps and perform kriging. STATISTICA '99 edition 5.5 was adopted for general statistical proposes.

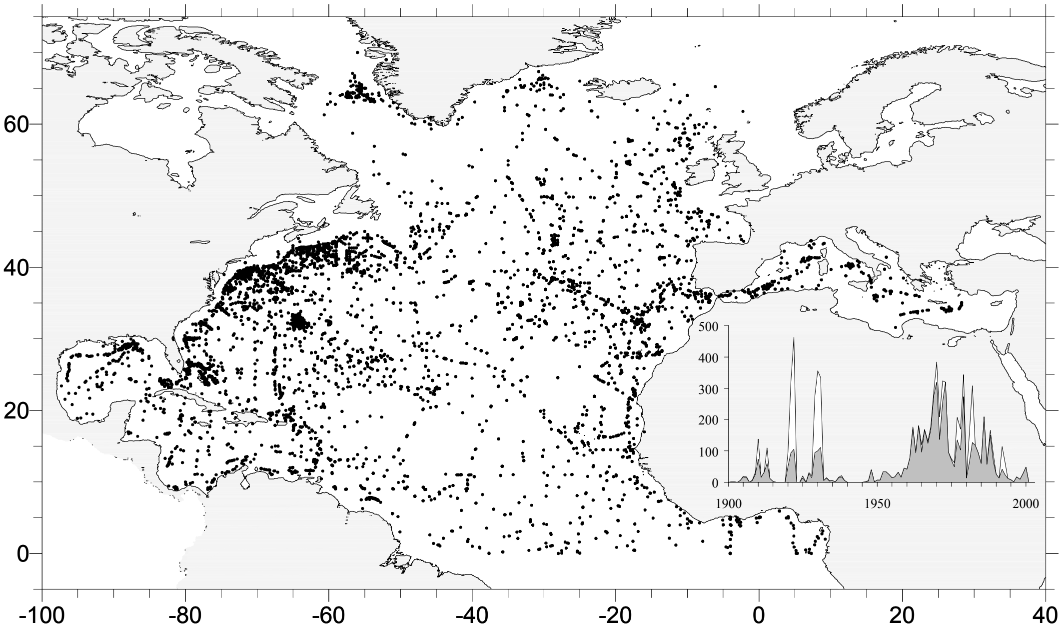


Figure 2.3 Geographical distribution of stations incorporated in the *S_db* (with positive catch of Stomiidae). One station can correspond to more than one net-haul (*field_code*). The insert shows the number of net-hauls (*field_code*) (white area) and stations (grey area) per year (from 1900 to 2000).

The extent of the data

The amount available. The Stomiidae database contains 141 species (i.e. those recognised as valid in 2001; see Chapter 5). The total number of records was 19727, representing at least 57000 specimens. Occurrences are reported from 8185 net-hauls carried out at 5832 stations (Fig 2.3). The collections covered most of the North Atlantic over 188 years (1812 to 2000), and peaked in the 1920's and 1930's and in the 1960's to 1980´s. A great variety of gears have been coded (ca. 180) but only a small subset of 20 was considered relevant sampling devices (Chapter 3 and 4).

Quality. Surveys targeting fauna other than midwater micronekton produced stomiids records on an irregular base. Those records are generally associated with low quality cruise data. Low quality data are also associated with many of the data incorporated from published material. However, quality varies from one collection catalogue to another (see Appendix B). A raw summary of the material included in the database follows:

Number of *field_code* with:	n (% total number of *fiel_codes*)
Year of capture	8014 (97.8%)
Month and season of capture	7910 (96.6%)
Time fishing	5973 (72.9%)
Light/dark period	6005 (73.3%)
Sampling depth	7455 (91.0%)
Gear_code with specifications	6598 (80.6%)
Complete cruise data	5392 (65.8%)
Records with complete cruise data	13949 (70.8%)

Chapter 3 - Sampling micronekton fish in the pelagic biotopes of the North Atlantic: gears description and fishing strategies (an historical approach using occurrences of stomiid fishes as a proxy)

Introduction

Pelagic nets are the principal sampling devices used to study the midwater organisms. Plankton ring nets (e.g. Beebe, 1931a; Schmidt, 1929; Tåning, 1944) rectangular micronekton nets (e.g. Davies and Barham, 1969; Devereaux and Winsett, 1953; Clarke, 1969; Wiebe et al. 1985) and commercial midwater trawls (e.g. Harrisson, 1967; Krefft, 1974, 1976; Magnússon, 1996; Themelis, 1996) are types of nets that have successfully sampled micronekton fish (>3cm). The gears directed at sampling meso- and mega- plankton also catch micronekton but at low rates, while the large commercial trawls sample predominantly within the size classes of most micronektonic and nektonic fishes but often fail to sample the smallest species (e.g. *Cyclothone* spp). Micronekton trawls are intermediate in size and size-dependent capture efficiency and were designed specifically to target these types of organisms. Remotely operated systems (both codend devices and opening-closing nets) to sample micronekton organisms at discrete depths have been developed and refined since the mid 1960's (Foxton, 1963; Aron et al., 1964; Clarke, 1969; Baker et al., 1973; Roe and Shale, 1979; Wiebe et al. 1985; Sameoto et al., 2000).

The pelagic samples obtained by nets are biased by the variability of a highly dynamic environment and biota, and by the selectivity of the gear used. The main objective of most pelagic investigations is to describe the natural variability and not the bias. The selectivity of the gears depends of their size, shape, structure and net features (i.e. colour and mesh size), and of the sampling methodology adopted. Tow speed, length and depth profile, along with the time of the day, are aspects that can determine the catch composition and relative species abundance in a sample.

Some reviews inventory and characterise the gears used to investigate the holopelagial biota, especially zooplankton (e.g. Harrisson, 1967; Clarke, 1977; Fraser, 1968; Kashkin & Parin, 1983; Sameoto et al., 2000). None of those papers or reports gives systematic details about the equipments used to sample the midwater micronekton fish.

This contribution aims to inventory and characterise the gears most often used to sample the micronekton midwater fish in the North Atlantic. This section also provides metadata about the programs that target the midwater fish biology and sampled the realm with the gears inventoried (i.e. cruises, dates, geographical coverage, depth profiles etc.; Appendix D)

Material and methods

Data source: the Stomiidae database

The data were extracted from a database that contains the occurrences of Stomiidae fishes in the North Atlantic and cruise data associated with those records (the *S_db*) (see Chapter 2 and Appendix C). Data were compiled from North America and European ichthyological collections and from a selected bibliography. Cruise data included vessel name, cruise reference, station and net-hauls codes (= *field_code*), station position, gear, date, time, fishing time and depth range sampled. A net-haul (= *field_code*) was regarded as the sampling unit. The database also contains gears specifications (e.g. name, acronym, and type, open or opening closing mechanism, mouth area, and mesh size). Raw data on gear and cruise data were corrected and improved by crossing referencing the ichthyological catalogues with published information (Chapter 2; Appendix B; Table 3.1).

Gear classification

Gears were classified as bottom trawls (*bt*), commercial midwater trawls (*c_mwt*), non-closing (*m_mwt_o*) and opening-closing (*m_mwt_oc*) micronekton midwater trawls, plankton midwater trawls (*p_mwt*) and neuston nets (*nn*). Other codes were also defined to accommodate unspecified midwater trawls, other samplers (e.g. fish traps, detritus sampler, fish catchers mounted in submersibles, SCUBA, vertical plankton nets, high speed nets, fishes washed ashore, fishes in stomach contents) and records without gear data.

Many of the gear types originally entered into the database under different notations, were merged after a critical evaluation of the range of gear types, reducing the total variety. For example, the DANA expeditions sampled with three sorts of 2m diameter ring devices that utilised different net materials (S200, P200 and S200x) but had the same or similar mesh-size and were fished in the same way. Other authors gave other notations for their 2m ring nets (e.g. Y200). Rationalisation of the database grouped all the ring nets into five categories according their diameter: R1m; R1.5m; R2m; R3m; R4m. The first three were classified as plankton trawls, while the R3m was considered a micronekton trawl. The very large ring net R4m was seldom used because it was difficult to handled.

There are various versions of the $8m^2$ rectangular midwater trawl (RMT 8) (Clarke, 1969; Baker et al., 1973; Roe and Shale, 1979; Table 3.1). Even knowing that the three opening-closing systems of that gear perform differently, it was practical to group them under the same gear code. This combination was based on the assumption that their fishing characteristics are similar when compared with other types of gears. The non-closing RMT 8 version was coded separately.

Because the net 1 of the MOCNESS 10 and MOCNESS 20 fished along a trajectory from surface to the deepest layer (as a half path of a double oblique tow of a non-closing trawl) the hauls made by those nets were coded separately from those made by the nets that fished at discrete depths.

Selection of principal gears and cruise data

Only a selection of gear types were fully describe; the selection criteria were: the frequency they were used (i.e. number of net-hauls), and the quality of cruise and specimen data associated with them. The full descriptions of those gears, along with instrumentation, operation methods and gear behaviour were then compiled from literature (Table 3.1). Data extracted from the database include cruises made, the amount and the quality of the data produced, the geographical coverage, the depth profile, the night/day sampling period and the time-fishing (Appendix D). Stations were linked to the Longhurst's (1995, 1998b) eco-biogeographical classification system.

Data description

Relative importance of the different types of gears

Originally 180 codes were assembled in the database to distinguish the gears that produced the reported stomiid catches. About 40% were bottom trawls and the

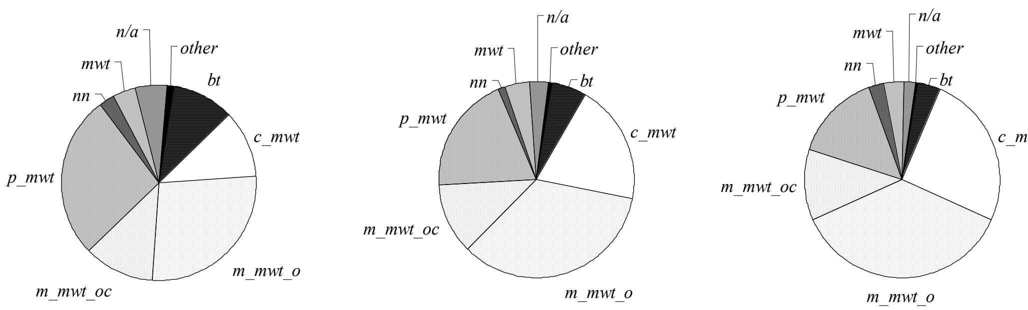
Table 3.1 Specifications of selected midwater gears frequently used to sample the North Atlantic midwater fishes during the 20th century. 1. gear type full name; 2. nonclosing or open-closing devices; 3. gear acronym; 4. net opening area (m2) (vary with towing speed); 5. fore net mesh size (cm); 6. cod end mesh size (cm); 7 average speed of towing vessel; 8. references on gear specifications, operation and behaviour; 9.observations, comments and additional information.

1	2	3	4	5	6	7	8	9
Engel Midwater Trawl		EMT 1400	600	20.3	1.3		Gibbs & Karnella, 1987	Modified from commercial (herring) epipelagic trawls (Schärfe, 1964). Numbers refer to meshes at forenet circumference. Meshes graded to cod-end. Two trawl boards and double towing wrap. Headline with floats and weights at the bottom line. Equipped with a “netzsonde”. *The dimensions referred by Gibbs & Karnella (1987) for the EMT 1400 seem too big (3127 m^2). Fishing with those nets requires the use of large stern trawlers. Clarke (2003) refer to a EMT used in 1963 RRS “Discovery II” with ca. 800 m2 (40*20 m), 100 aluminium floats on its headrope, 500 kg of chain on its footrope and 2 doors weighing 750 kg (see also Harrisson, 1967).
		EMT 1400	600*	20	1	2.5–3.5	Krefft, 1974, 1976; Post, 1987	
		EMT 1400	600	81.3	0.2		McKelvie, 1985a	
Young Fish Trawl		IYGPT 100	100	60	1.25	2.5	Hislop, 1970; Koeller & Carrothers, 1981	Modified from commercial trawls (Barraclough & Johnson, 1956, 1960) to sample young fish of commercial species. Single warp; two trawl boards; floats on head line and weights at bottom bridles; bridles, boards and wrap ahead of the mouth. Equipped wit a telemetered net sounder
		YFT 100	100	60	1.25	3		Modified from commercial trawls to sample young fish of commercial species. Two trawl boards and double towing wrap. Headline with floats and weights at the bottom line. Equipped wit a telemetered net sounder.; Electronic depth-time recorder.
Isaacs-Kidd midwater trawl	non-closing	IKMT 10'	7.8	1.2	0.075	3	Isaacs & Kidd, 1953; Devereaux & Winsett, 1953; King & Iversen, 1962; Michel & Grandperrin, 1970; Foxton, 1969; Brooks et al., 1974; see also Backus et al., 1970, Gibbs & Karnella, 1987	The first and widely used midwater trawl. Considered as a semi-quantitative gear (Foxton, 1968; Kashkin & Parin, 1983). A frameless gear characterized by its large vane depressor. Bridles in front of net mouth. In former times it was fitted with a graded mesh size net i.e. half-lined; in most of tows however the outer mesh was full lined. Fish perpendicular to vertical. Pay out/ haul-in: 40-60 m/min. Estimated volume of water filtered: 3.62 * 104 m3 / h (assuming 7,08 m2 moth area; 3 miles/ h tow speed; and 92% filtering efficiency - Brooks et al., 1974; Brooks & Saenger, 1991); The discrete depth sampler (DDS) are cod-end device such as the catch dividing bucket (Foxton, 1963) and the four-chambered discrete depth sampler (Aron et al., 1964); both depth telemetered; equipped with a depth/time recorder (TDR). References also relate to IKMT 6’.
	open-closing (cod end)	IKMT 10' DDS	7.8	0.95/ 0.5	0.05	2.5–3.5		

1	2	3	4	5	6	7	8	9
Multiple Opening/ Closing Net and Environmental Sensing System	net 1	MOC 10 N1	10	0.3	0.3	1.5-2	Wiebe et al, 1985; Sameoto et al., 2000	A rigid frame device based in the Tucker Trawl. The first MOC versions targeted meso- macrozooplankton (Wiebe et al., 1976). The underwater electronics package is equipped with environmental and net behaviour sensors; may carry other electronics and cameras. Controlled electronically through a conducting towing wrap. Micronekton versions equipped with 5 to 6 nets (up to 10 in MOC 10). Net 1 (N1 net-hauls) samples from surface to depth. Filter ca. 30000 and 60000 m^3/ hour (MOC 10 and 20); Pay out 0.5 m/s; haul 0.5 to 1.0 m/s. Mouth area at 45° towing angle, at about 2knots. Implies the use of large vessels. MOC 10: 3.4x4.6m; 640 kg; MOC 20: 5.5x7.3m; 900 kg.
	open-closing	MOC 10	10	0.3	0.3	1.5-2		
	net 1	MOC 20 N1	20	0.3	0.3	1.5-2		
	open-closing	MOC 20	20	0.3	0.3	1.5-2		
Ring-trawl		R 3m	7.07	2.4	1.2	2.5-3	Schmidt, 1929; Anon., 1934; Tåning, 1944	A conical net normally attached at the deeper position in a set of 5 ring nets, often alongside several R1.5m or R2m.
Rectangular midwater trawl	nonclosing	RMT 8	8	0.45	0.033	2	Clarke, 1969; Baker et al., 1973; Roe & Shale, 1979; Roe et al, 1980; see also Clarke & Pascoe, 1985	A family of rectangular hanging frame midwater trawls with weights at the bottom bar. The most common is the RMT 8. The first version fitted one opening closing net; the multi-net system (3 nets) appeared later; the RMT 8+1 system coupled $1m^2$ and $8m^2$ nets (RMT 8+1). The open-closing versions were grouped as RMT 8 MC. The system is controlled acoustically and can be equipped with environmental and net behaviour sensors. RMT 8 MC fish at an angle of 45° at about 2 kn (61° the RMT 8+1). Filter ca. 25000 m^3/ hour; pay out 0.5 m/s; hauled 0.5-1.0 m/s. Several nonclosing versions were built (RMT 8, 10, 25, 50, 90). Various cod-ends systems were designed to these devices (i.e Aldred & Wild, 1979). The system can fish to 4500 m depth.
	open-closing	RMT 8 MC	8	0.45	0.033	2-2.5		
	nonclosing	RMT 10	10	0.45	0.033	2		
	nonclosing	RMT 50	50	1	0.033	2		
Tucker trawl	open-closing	TT 5	5	0.16	0.055	2-3	Davies & Barham (1969); Hopkins et al., 1973; Themelis, 1996	The first open-closing device with unobstructed mouth. Carries up to 9 nets. Fishing area aprox. 3.5 m^2 at 2,7 knots at 10 m depth; probably almost vertically at deepest depth. Controlled by a conducting cable or by a telemetry unit; Time-Depth Recorder (TDR) and flowmeter.
Isaacs-Kidd midwater trawl		IKMT 6'	3	1.2	0.05	3-4	Aron et al., 1964	See references and observations in IKMT 10'entry;
Ring-nets		R1m	0.79	0.2	0.2	2.5-3	Beebe, 1931a	Normally used in an array of six nets attached at equal distances Includes gears previously classified as net 1msilk, P100 and S100.
		R2m	3.14	0.2	0.2	2.5-3	Schmidt, 1929; Anon., 1934; Tåning, 1944	Includes gears previously classified as starmine net 2m, S200), S200x and Y200. Fishing net use normally attached to a set of several ring nets, often with a R3m at the end of the array
		R1.5m	1.77	0.2	0.2	2.5-3		Includes nets classified as P150, PS150 and S150. Fishing net use normally attached to a set of several ring nets, often with a R3m at the end of the array
Neuston net		NN	0.79	0.05	0.05	3-4	Backus et al., 1970; Gibbs & Karnella, 1987	Ring net trawled from the side of the ship, half submerged, often during midwater trawling (see also Bartlett & Haedrich, 1968)

remaining were classified as commercial, micronekton and plankton midwater trawls (ca. 17% each) and other gear types (8%).

Bottom trawls represent 10% of the net-hauls but a smaller proportion (<10%) of the occurrences and specimen reported. The gears classified as midwater trawls were responsible for ca. 85% of the net-hauls, 90% of the stomiid records and 94% of the specimens caught (Fig. 3.1). About 10% of the records were associated with unspecified midwater trawls (*mwt*), other gears, and gear not available.



a) b) c)

Figure 3.1. Basic data per gear type included in the *S_db* (percentage). a) number of net-hauls (= *field_code*) (n=8185); b) number of records (n=19727); c) number of specimens (n=57000). *bt*: bottom trawls; *c_mwt*: commercial midwater trawls; *m_mwt_o*: non-closing micronekton midwater trawls; *m_mwt_oc*: open-closing micronekton midwater trawls; *p_mwt*: plankton midwater trawls; *nn*: neuston trawl; *mwt*: unspecified midwater trawls; *n/a*: gear not available; *other*: other samplers.

The number of net-hauls completed with non-closing micronekton and plankton trawls was similar, while those undertaken by discrete micronekton trawls almost equal the ones carried out by commercial trawls. Despite the number of hauls linked with plankton gears being more than twice that of commercial trawls, the later were responsible for about the same number of records and for almost twice the fish caught by the former. Micronekton midwater trawls (both open-closing and open nets) comprise slightly less than 50% of the records and specimens incorporated in the database. Neuston samples contribute to ca. 2.5 % of net-hauls and specimens.

Selected midwater trawls

Twenty midwater trawls were selected for further descriptions. They include five commercial trawls, ten micronekton trawls (five open-closing devices), four plankton trawls and the 1m diameter neuston net. The commercial trawls include three Engel midwater trawls (EMT 1600, EMT 1400 and EMT 630-80) and two young fish trawls

(YFT 100 and IYGPT 100). The non-closing micronekton midwater trawls include the Isaacs Kidd Midwater Trawl (IKMT 10’), the rectangular midwater trawls (RMT 8, RMT 10 and RMT 50) and the ring net with 3m diameter (R3m). The opening-closing systems comprise the IKMT 10’, equipped with cod-end discrete depth samplers (DDS), the assemblage of three versions of the RMT 8, the Multiple Opening/ Closing Net and Environmental Sensing Systems (MOCNESS 10 and MOCNESS 20) and the Tucker trawl (TT 5). The selected plankton samplers were the ring nets with different diameters (R1m, R1.5m and R2m) and the non-closing IKMT 6’. Separated entries were considered for the open nets of the multi-net samplers MOCNESS 10 and 20.

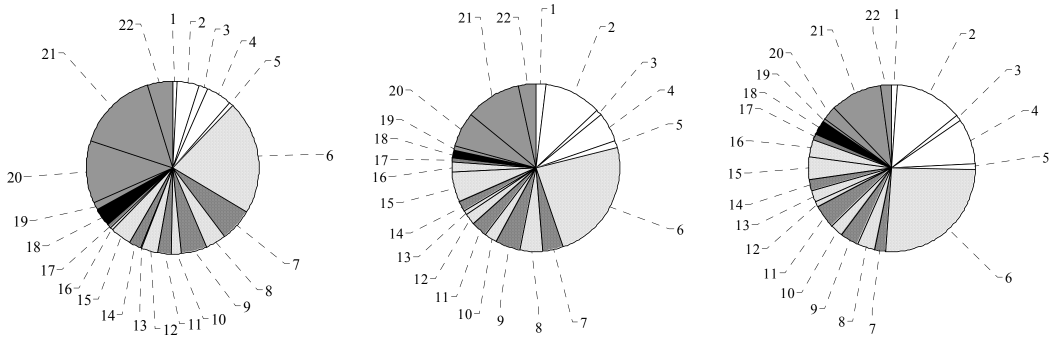
The selected gears differ in their structure, size, net type and mesh size (both at the forenet and cod-end), presence or absence and type of opening-closing systems and the nature of the electronics used (Table 3.1).

The mechanism to close and open the nets in depth discrete samplers considered here are remotely triggered, acoustically (RMT 8 MC) or through a conducting cable (MOCNESS). Those devices are normally equipped with sensors that measure environmental properties and produce information about gear behaviour and sampling conditions. Most of the probes used in oceanography (e.g. CTD [temperature, conductivity/ salinity, dissolved oxygen], depth, photometer, fluorometer, acoustic systems) as other equipments such as video cameras can be mounted in fishing devices. Net speed and volume of water filtered are normally measured with flowmeters. Net-sounders give the distance between the net and the bottom (altimeters) and information about the behaviour and area of the net mouth. These types of equipment are also used in open nets, both micronekton and large pelagic trawls.

Relative importance of the selected gears

The selected gears represent 72% of the net-hauls, 80% of the stomiid records and 83% of the specimens reported.

The IKMT 10' was responsible for more than 20% of the net-hauls and for about 25% of the records and fish caught (Fig. 3.2). Following in terms of amount of net-hauls were the R2m and R1m, which normally fished as part of a long array of nets. Then a group of nine gear types accounted individually for 6% to 3% of the net-hauls and other five were responsible for 3% to 1% each. Finally the remaining five gears were responsible all together for less than 6% of the net-hauls recorded. In terms of number of records and specimens, the relative importance of the ring nets decrease (especially that of the R1m), and the contributions of the EMT 1600, IYGPT and to some extend of the RMT 10, MOC 20 and MOC 10 increased. The RMT 50, and the RMT 8 supplied the lowest numbers of net-hauls, the IKMT 6' and the TT 5 the lowest numbers of records and the EMT 630 and the IKMT 6' the lowest numbers of specimens.



a) b) c)

Figure 3.2 Basic data (percentage) per gear selected included in the Stomiidae database (*S_db*). a) number of net-hauls (=*field_code*); b) number of records; c) number of specimens. 1: EMT 1400; 2: EMT 1600; 3: EMT 80-630; 4: IYGPT; 5: YFT 100; 6: IKMT 10'; 7: IKMT 10' DDS; 8: MOCNESS 10 N1; 9: MOCNESS 10; 10: MOCNESS 20 N1; 11: MOCNESS 20; 12: R 3m; 13: RMT 8; 14: RMT 8 MC; 15: RMT 10; 16: RMT 50; 17: TT 5; 18: nn; 19: IKMT 6'; 20: R1m; 21; R2m; 22: R 1.5m. (See Table 3.1 for full names of gears). White sectors: commercial midwater trawls (1-5); dotted sectors: micronekton midwater trawls (6-17) (darker: opening-closing systems); black sector: neuston net (18); grey sectors: plankton midwater trawls (19-23).

Geographical distribution of sampling

Some gears were used extensively to sample the North Atlantic mesopelagial, while the use of many was restricted to certain geographical areas (Table D.1 and maps in Appendix D). Only the IKMT 10’ sampled throughout all the North Atlantic provinces of Longhurst (1998b), except the BPLR and SARC. The R2m was also used throughout most of the basin (10 provinces) and the EMT 1600, R3m and R1.5m sampled 7 provinces. Other widely used gears include the RMT 10, the NN and the IKMT 10' DDS (6, 6 and 5 provinces, respectively). The remaining trawls sampled at three (YFT, MOCNESS 10 and R1m), two (EMT 80-630, RMT 8, RMT 8 MC and IKMT 6'), or one (EMT 1400; IYGPT; MOCNESS 20, RMT 50; TT 5) biogeographic provinces.

Clearly, the North Atlantic Subtropical West (NAST W) was the province with the best sampling coverage, where most of the gears were used (Fig. 3.3). The moderately sampled GFST, NAST E and CARB provinces were fished by more than 50% of the devices considered. NATR, NADR and WTRA ranked next considering the number of net-hauls. The CNRY, ARCT, ETRA and SARC provinces were sampled by less than 100 net-hauls and only by 2 to 4 samplers. A considerable number of tows were made at MEDI but only by the IKMT 10' (both open and open-closing versions) and R2m.

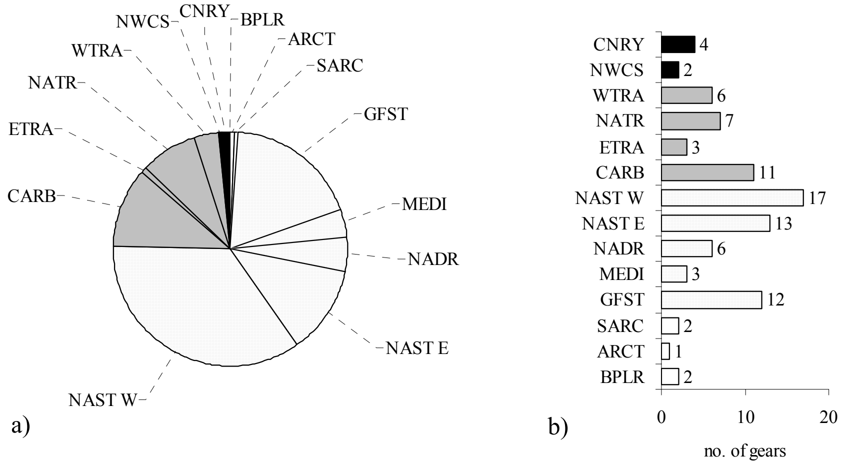


Figure 3.3 a) Number of net hauls (= *field_code*) (percentage) and b) number of selected gears (n=22), per Longhurst's (1998b) biomes and provinces (see Fig. 2.3 for acronyms or List of Acronyms). White: Polar Biome; dotted: Westerly Winds Biome; grey: Trade Wind Biome; black: Atlantic Coastal Biome.

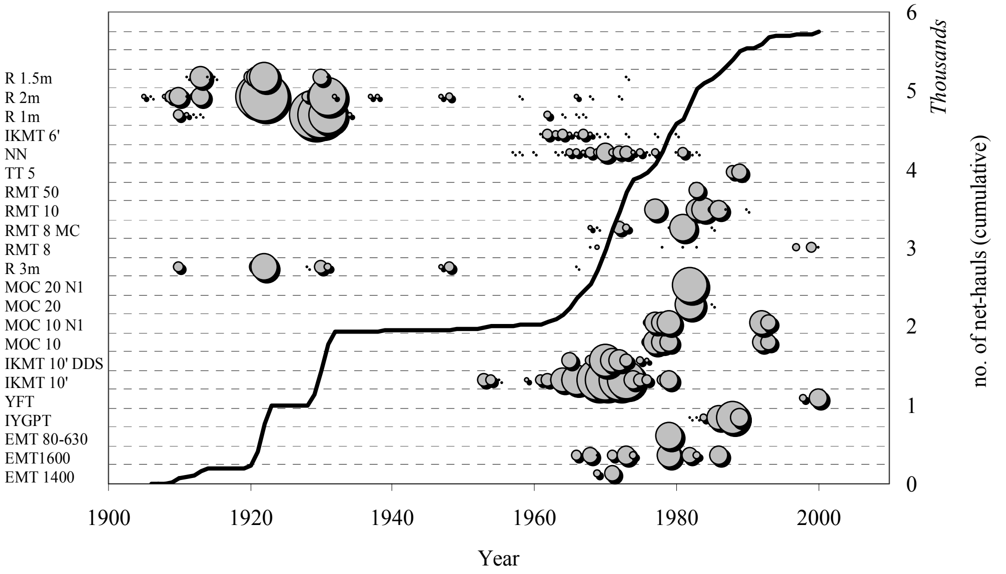


Figure 3.4 Distribution of net-hauls per selected gears and per year. Bubbles are proportional to number of net-hauls. Black line: cumulative number of net-hauls.

Temporal distribution of sampling

Sampling was not evenly distributed through time (Fig. 3.4). During the 20th Century the distribution of net-hauls showed two main periods of mesopelagic research. The first, between 1909 and 1931, was largely marked by the Danish Expeditions sailing on “Thor”, “Margrethe”, “Dana I” and “Dana II”. Sampling peaked in the early 1920s and 1930s, with sets of ring nets. Then the research on North Atlantic midwater fauna was interrupted for more than 20 years, as a consequence of the II World War. A decade after that dramatic episode a second bloom of deep-sea pelagic surveys began, involving several countries, mainly the USA, Germany, Canada, Russia and UK. The activity peaked in the 1970s and 1980s, declining thereafter. It was through the later period that rectangular micronekton and commercial trawls were introduced as pelagic samplers. In the North Atlantic, opening closing devices have been utilised regularly since 1965.

Fishing strategies

Cruise data provided information on the sampling strategies adopted. Most of the research programs created their own specific sampling methodology. The variability was so high that to group devices that share similar combinations of depth strata sampled, day versus night hauls and haul length was a difficult task (Fig. 3.5). However, most of the programs had a relatively consistent sampling strategy.

Depth. Midwater sampling surveyed mainly the epi- (36%) and the mesopelagic (47.5%) layers down to 1000m depth. The net-hauls that fished the bathypelagial (1000-3000m) represented 15% of the total hauls reported. Those in the epipelagial were made mainly during night time and sampled the interzonal migrating micronekton fish. The upper (200-400m) and middle (400-800m) mesopelagic layers were surveyed by a similar number of hauls (ca. 18% and 22%, respectively). The remaining 8% of the tows sampled the lowest horizons of the mesopelagial (800-1000m). In this dataset very few net-hauls reached the abyssopelagic layers (>3000m; ca. 0.2%).

The EMT 80-630, YGPT, RMT 8, RMT 10 and R2m sampled mainly the epipelagic and the upper mesopelagic layers. The other gears also surveyed the middle and the lower mesopelagial, but some (i.e. R3m, RMT 50, R1m and R1.5m) show particular depth profiles. Opening-closing systems (except the TT 5) fished regularly throughout the water column to 1000m. The day and night depth sampling profiles were different;

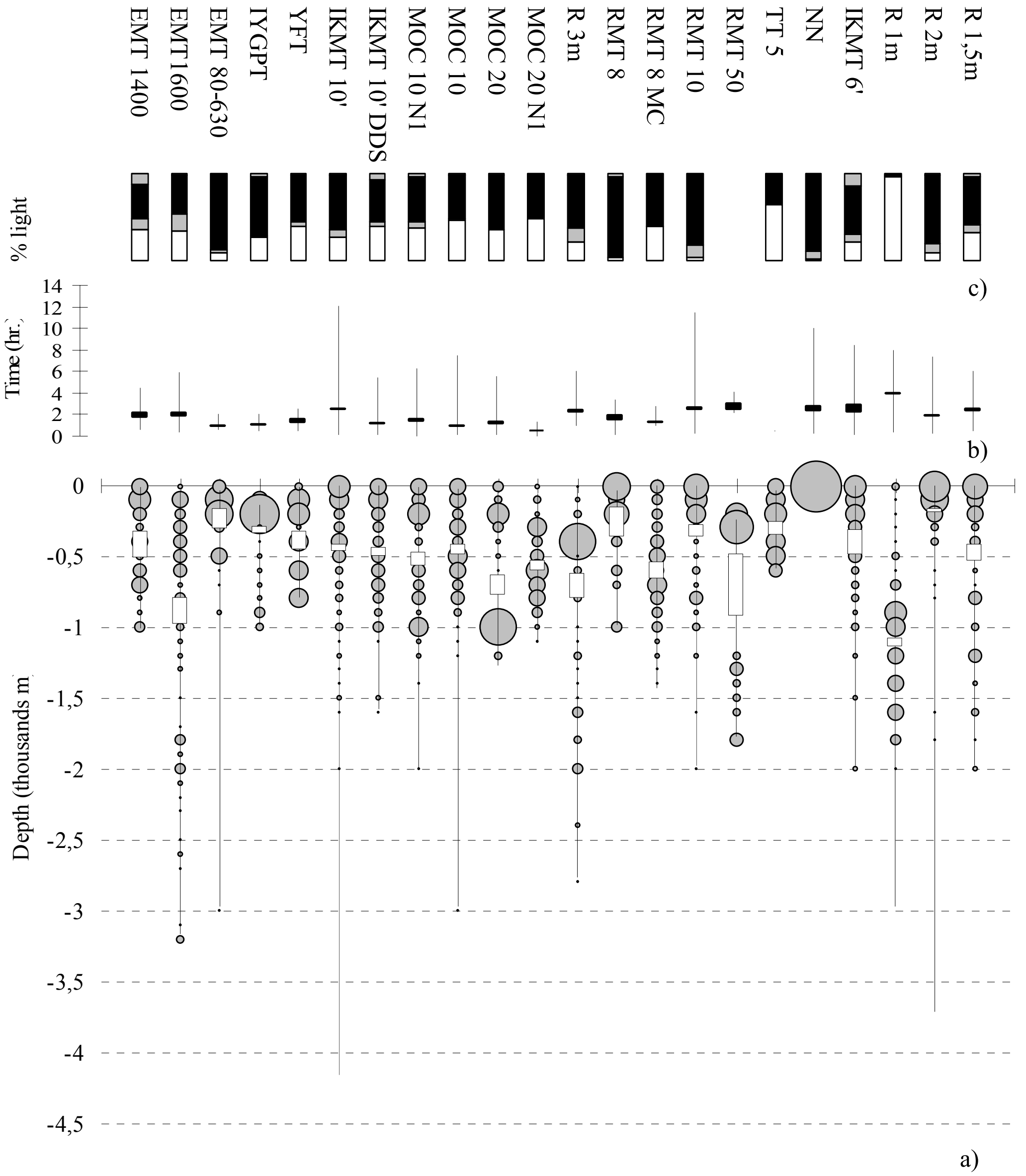


Figure 3.5 Summary of cruise data from selected gears (see Appendix D or List of Acronyms for acronyms). a) depth distribution of hauls by 100m depth classes (bubbles size represents percentage); 95% confidence limits of mean (white box) and maximum and minimum depth values (black lines). b) mean, maximum and minimum fishing time. c) percentage of day (white), night (black), dusk and dawn (grey) hauls.

most of the open nets fished by night normally at shallower depths while those performed during day time at the deeper layers. The opening closing nets sampled regularly throughout the water column both by day and night.

Time fishing. Two hours were the average fishing time for the EMT 1600, EMT 1400 and R2m hauls. The other commercial trawls fished for shorter periods (YFT = 1:24; IYGPT = 1:02; EMT 80-630 = 0:54). The duration of an average haul made by the open midwater trawls ranged from 2:45 (RMT 50) to 1:51 (RMT 8) and the IKMT 10', RMT 10, IKMT 6', R1.5m and NN lasted for around 2:30. The IKMT 10' DDS, MOC 10 and RMT 8 MC standard hauls took in average around one hour (1:15-0:56), while the MOC 20 lasted ca. 30 min. The average time that the MOC 10 and MOC 20 systems needed to reach the lower strata of a haul was 1:27 and 1:12, respectively. However, the R1m was the device that has been trawled for the longest periods (i.e. about four hours).

Light conditions. Considering the light conditions under which the tows were made, the R1m and the NN were generally used under the opposite conditions. The first net was trawled almost entirely during the day and the later exclusively during the night. The EMT 80-630, RMT 10, RMT 8 and R2m caught stomiids mainly during night time in the upper layers of the ocean. The IYGPT, IKMT 10' and R3m show a high proportion of night hauls, with some twilight hauls. The 4 multi-closing gears (all but the TT 5), the YFT, and R1.5m show a relatively balanced ratio between day and night hauls. The EMT 1600, EMT 1400 and IKMT 6' had a considerable numbers of dawn and dusk rows. There were no data concerning the period of the day the RMT 50 was deployed.

Conclusions

The compiled data produced a representative set of sampling programs that targeted the North Atlantic pelagic waters. Although the Stomiidae database does not include data from several midwater sampling programs (see Chapter 4), the assembled material includes the most relevant pelagic samplers used to study the micronekton in the North Atlantic.

A panoply of devices caught midwater fishes in a more or less efficient manner. Historically, midwater sampling was limited by the technology available to construct sampling equipment and instrumentation (e.g. electronics) and also by the trawling capacities of the research vessels. The development of more effective gears generally replaced the older technologies and equipment. The arrays of ring nets used extensively during the first decades of the 20th Century (Beebe, 1933a; Schmidt, 1929; Anon., 1934; Tåning, 1944) are no longer employed to catch micronekton. Since the 1960's the programs directed at this fauna have used rectangular midwater trawls or large commercial pelagic trawls modified to sample this group of organisms. The Isaacs-Kidd-midwater trawl (IKMT) was the first gear built specifically to sample micronekton (Devereaux and Winsett, 1953; Isaacs and Kidd, 1953; Harrisson, 1967). However, it has bridles in front of the net mouth, which is a characteristic considered undesirable as it causes fish avoidance (Clarke, 1969, 1977). Moreover, the gear can not be opened and closed at discrete depths, a limitation that was partially resolved by the invention of cod-end discrete samplers (Foxton, 1963; Aron et al., 1964; Pearcy and Hubbard, 1964). Even so the IKMT (transformed or not) was used all over the world over a number of decades and one time it was considered the standard sampler for micronekton studies (Foxton et al., 1968). However, soon after that the Tucker trawl (TT) appeared (Davies and Barham, 1969) to resolve the problems detected with the IKMT. This trawl has an unobstructed mouth and allowed the opening and closing of one or more nets that slide along its rigid frame. Although it was considered an important improvement to sample the midwater fauna the TT was not adopted by the majority of the researchers that study the North Atlantic pelagial. The exceptions were the South Florida University team that used the net to a long-term study of the micronekton from the Gulf of Mexico (Hopkins et al., 1973; Gartner et al., 1988; Hopkins and Sutton, 1998; data only partially available for this study) and a number of surveys made in the Slope Water off Canada (Themelis, 1996; Appendix D). The opening-closing mechanism designed made the use of cod-end discrete depth samplers much less attractive (except in large pelagic trawls and when one wants to reduce mechanical damage and heat shock to deep-sea animal during the ascent of the net; e.g. Childress et al., 1978). The rectangular midwater trawl (RMT 8; Clarke, 1969) came out soon after the Tucker trawl. It combined an operational advantage of the IKMT (i.e. the absence of a rigid frame) with an efficient opening–closing system. Moreover, the RMT 8 system was equipped with newly developed acoustically controlled electronics which allowed for a better monitoring of the fishing operations and of the environment. This feature permitted the device to be used to sample well within the abyssopelagial (i.e. to 4500 m; Roe et al., 1980). The larger non-closing versions of the RMT (i.e. RMT 25, 50 or even 90) were not widely used but it seemed to be operational according to the versatility of the design (Baker et al., 1973;

Clarke and Pascoe, 1985). However, the manoeuvrability of those nets (especially the RMT 50 and 90) probably needs to be tested and improved. The MOCNESS series appeared later as an improvement of the basic plans of the Tucker trawl (Wiebe et al., 1976, 1985; Sameoto et al., 2000). Those gears with rigid frames were equipped with more sophisticated sensing apparatus, which permitted a better monitoring of net performances and of the sampled environment. The communication between the device and the surface is through a conductor cable, which guarantees a high quality data transmission but limits the depth of its operation. The MOCNESS are less manageable than the RMT 8 but they give a more accurate picture of their sampling efficiency. The RMT 8 systems (especially the RMT 1+8M; Roe and Shale, 1980) and the MOCNESS are the most sophisticated opening-closing micronekton multi-net gears currently available. These devices greatly decrease the time needed to sample the water column and the time gap between consecutive samples. Those features are important to characterise the structure of the highly dynamic pelagic community. The operation with a MOCNESS 20 requires a large research vessel.

During the late 1950’s large midwater trawls started to be regularly employed to sample the mesopelagial (Harrisson, 1967). Several models of the commercial Engel trawls (EMT) were used to sample along large geographical transects (Krefft, 1974, 1976; Post, 1987) or to study the composition of the fauna from a particular region (e.g. McKelvie, 1985a; Gibbs and Karnella, 1987; Post, 1988). Fishing with large commercial trawls requires the use of large and powerful trawlers, which are not common in the scientific fleets of most countries. An alternative to the larger trawls is the young fish trawls, as the IYGPT, which sampled very efficiently the midwater fauna (Chapter 4). These trawls are more easily manoeuvred and can be operated by much smaller vessel. The young fish trawls evolved from commercial midwater trawls for herring (Barraclough and Johnson, 1956 1960), which were later modified by fishery biologists to assess recruitment of commercial species (e.g. gadoids; Hislop, 1970). These midwater samplers were recently used for many pelagic studies that did not require vertical discrimination of the midwater fauna. (i.e. Moore et al., 2001, 2002, 2003b, 2004 in the Bear Seamount; Pusch et al. 2002, 2004 in the Northeastern Atlantic seamounts; Bordes et al., 1999 and Wienerroither, 2003 in the Canaries islands). They are easily operated, carry sophisticated electronics and be towed by relatively small research vessels.

Profiting from the developments promoted by important deep midwater fisheries and international fishery biology surveys (e.g. directed to *Sebastes* sp. in the Irminger Sea), large research vessels are using huge pelagic trawls, equipped with sophisticated acoustic apparatus, for micronekton investigations. The Gloria (Magnússon, 1996; Sigurðsson et al., 2002), the Åkra and the Egersund trawls (operated during the “G.O.Sars” 2004 MAR-ECO; Bergstad & Godø, 2003) are examples of nets recently employed to study the midwater fauna (data not included in this survey). Even if the samples taken by cod-end discrete samplers are in general contaminated, the utilization of those devices (e.g. similar to multiple plankton sampler) in commercial trawls (as during the “G.O.Sars” 2004 MAR-ECO cruise) can give indications concerning the vertical distribution of the organisms.

The main weakness of those large samplers is the difficulty of quantifying the escapement and extrusion of micronekton fishes (Gjøsaeter and Kawaguchi, 1980; Pearcy, 1980). A possible evaluation of that is to line fully the commercial trawl as Stein (1985) reported.

The sampling strategies developed to sample the oceanic micronekton fish were quite diverse. The programs had different scientific goals and the teams developed the methodologies accordingly. Quite often, however, the scientific parties faced logistic constraints and the sampling strategies followed a compromise between the desirable and the possible. For example many programs included several scientific teams and only one of the activities to be done was midwater sampling, which was limited to a certain time period. Also the sampling methodology had to be adjusted to the scale of the study: biogeographic studies profit from the use of large samplers fishing by day and night across oceanic transects and targeting layers with maximum diversity and abundance of organisms; while studies aiming at investigating the vertical dynamics or the trophodynamics of pelagic micronekton benefit greatly from the use of multi-net open-closing trawls fishing obliquely at narrow discrete horizons at all times of the day at fixed stations. The differences and implications of these two sampling methods were analysed by Angel (1977). In general it is accepted that a detailed definition of a consistent sampling strategy is critical and should be guided by the specific objectives of the programs. For example, the recognised high quality of the IOS/ SOC (see entries for BMNH in Appendix B and RMT 8 MC in Appendix D) data is clearly related with the coherent standardization of sampling procedures followed by most of the programs carried out at the eastern Atlantic over more than one decade (e.g. Roe et al., 1984).

Improvements in sampling methodologies are needed together with an increase in the sophistication of observational methods. The quality of the data obtained by programs completed with midwater nets will profit from the integration of new technologies for monitoring the sampled environment and the net behaviour and performance. The improvement of the quality and availability of the data recorded will enhance the quality of the analyses produced and consequently of our understanding of the ecosystem. In the future there will surely be the development and use of sophisticated alternative methods such as optical and acoustic tools mounted in remote controlled underwater platforms (Parrish, 1999). These types of equipment will open other observational windows to investigate the deep-sea pelagic life, but nevertheless nets will remain the essential samplers to study the biology of most of the oceanic midwater fauna.

Chapter 4 – Sampling micronekton fish in the pelagic biotopes of the North Atlantic: comparative gear performances and fishing effort.

Introduction

Biologists first used ring nets to sample regularly the midwater fauna. They were trawled individually or in an array of various nets attached to a towing cable. After the II World War the first micronekton rectangular samplers were constructed. The Isaacs-Kidd midwater trawl (IKMT) became the most popular. The usefulness of the system was sufficiently high that an ICES/SCOR/UNESCO Working Party (Foxton et al., 1968) proposed the gear as the standard for sampling micronekton. The need to sample in discrete depth strata inspired the development of open-closing cod-end devices that were fitted to the IKMT (Foxton, 1963; Aron et al., 1964; Pearcy and Hubbard, 1964; Table 3.1). Not long afterwards, however, the recommendation was changed owing the development of new micronekton midwater sampling gear that proved to be more effective. The Tucker Trawl (TT; Davies and Barham, 1969; Hopkins et al., 1973) and the Rectangular Midwater Trawls (e.g. RMT 8 MC; Clarke, 1969; Baker et al., 1973; Roe & Shale, 1979; Roe et al, 1980) appeared first, then the Multiple Opening/ Closing Net and Environmental Sensing System (MOCNESS 10, 20; Wiebe et al, 1985; Sameoto et al., 2000).

Midwater trawls larger than ring nets have been developed since the first oceanographic expeditions in the 19th Century, but the pelagic micronekton fauna were not effectively sampled. Only after the 1960's did commercial trawls start to be successfully applied to study the realm (Harrisson, 1967). Today, the commercial trawls used to survey the pelagial, range from the small young fish trawls (Barraclough and Johnson, 1956, 1960; Koeller & Carrothers, 1981) to the very large trawls designed primarily for industrial fisheries (e.g. Gloria, Åkra and Egersund trawls).

The ICES/SCOR/UNESCO group (Tranter, 1968), reviewed the status of zooplankton (and micronekton) sampling methods used in the preceding 150 years. The main objective was to improve methodologies to better understand sampling performances and then the quantification of diversity, density, abundance and behaviour of life in the pelagic ecosystems. The concepts debated are still valid today and include: filtration performance and efficiency; organism's avoidance, escapement and extrusion; net selectivity (mesh selection); turbulence and disturbance; system variability and sample representativeness. The group also studied the relationships between the samples obtained and the size of the gear, mesh size, tow speed, tow length, sampling depth, etc. (Tranter and Smith, 1968; Clutter and Anraku, 1968; Tranter and Smith, 1968). These concepts should be addressed when analysing the catch made by any pelagic samplers, as they apply to all levels of the community spectra (Fraser, 1968).

Michel and Grandperrin (1970) and Barkley (1964, 1972) improved the theory on pelagic gear selectivity. Later Kashkin and Parin (1983), in their classical review, concluded that quantitative results obtained by non-closing nets are inevitably relative. The main problem is that the data do not give quantitative unequivocal data on the behaviour of deep midwater organisms.

Empirical studies concerning the selectivity of midwater samplers are scarce. Some programs compared the catches of a number of hauls made by the same net under different conditions (e.g. different mesh size or tow speed), other compared two gears fishing at the same region (e.g. Aron et al., 1964; Grandeperrin, 1967; Harrison, 1967; Aron and Collard, 1969; Michel and Grandperrin, 1970; Pearcy, 1980; Gartner, et al 1988). However, the effects of tow speed, mesh size, haul profile, etc., on the catches of midwater fishes are still poorly understood. None of those studies involved more than three gears and none was done in the last 15 years! In contrast, studies on the selectivity of commercial trawls on over exploited pelagic and demersal species are much more abundant.

The selectivity of a midwater sampler can be somehow quantified by analysing the catch obtained during field studies that were originally designed for a different purpose. It is accepted that larger trawls catch larger organisms, more micronekton specimens and probably more species. However, a generalized pelagic sampling theory does not exist today. The statement is reinforced by the lack of agreement between the results obtained from those empirical studies mentioned above. The complexity of the interactions between the samplers, the sampling procedures, the biota distribution and behaviour and the environment, is simply not described. However, if a significant sample size is achieved, a gear offers a representative “window” of a specific fraction of the biota that matches its selectivity (e.g. Angel, 1977). The option is to calculate an average haul composition and use this as the basis for making comparisons between gears without any assumption about the gear and its operation.. Nevertheless these comparisons should always be regarded as relative, and affected by an unknown bias, especially considering the inherent heterogeneity (patchiness) of the ecosystem under study.

This section aims to describe, compare and calibrate the fishing performances of selected midwater gears, by using data on stomiid fish occurrences as a proxy. The approach allows the sampling equipment to be ranked through the estimation of net-scores and then the relative sampling effort needed to produce the North Atlantic stomiid fish recorded.

Material and methods

Source data

The Stomiidae database (*S_db*) was assembled from historical ichthyological collections, selected bibliography and recent midwater cruises. The database is presented in the Chapter 2 and its structure detailed in Appendix C. It comprises North Atlantic occurrences of stomiid fishes and data about the cruises that produced those records. Cruise data include vessel name, cruise and station references, station geographical position, date, time of the day and fishing time, sampling depth range and gear used.

Basic data in relation to fishing gear comprise fields that code, classify, and characterise each device (see Appendix C). Chapter 3 detailed the diversity and the classification of the gears assembled, and the cruise data concerning the sampling programs made by 20 gear selected for further analysis. Those samplers were: 5 commercial trawls; 10 micronekton trawls (5 opening-closing systems); 4 plankton trawls; and the 1m diameter neuston net (Table 3.1). They were coded as: Engel Midwater Trawls (EMT 1600, 1400, 630-80); Young Fish Trawls (IYGPT, YFT); Rectangular Midwater Trawls (non-closing: RMT 8, RMT 10, RMT 50; multi-closing: RMT 8 MC); Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS: MOC 10, MOC 20); Isaacs Kidd Midwater Trawl (IKMT 10’, IKMT 6’, IKMT 10 DDS [with a cod-end device]); Tucker Trawl (TT 5); Ring nets (R1m, R1.5m R2m, R3m); and 1m ring neuston net (nn).

Data on gear specifications, instrumentation and operation were compiled from literature and summarised (Table 3.1). A detailed account of the cruise and catch data for the selected gears is provided in Appendix D.

Species (taxa), number and size range of the specimens are the basic biological data associated with each stomiid occurrence.

Basic data computation

A net-haul (coded by a *field_code*) was the sampling unit considered. The catch obtained by one net-haul is represented by one or more records, if more than one species had been caught during that net-haul. Each record (or species occurrence) has an associated number of specimens (*n_spec*) and their standard length range (*min_sz* and *max_sz* SL). The number of fish caught by one net-haul is the sum of the specimens of all taxa represented in that catch. The average size (*avg_sz*) of the fish from one record is the mean of the size range values. The size range of fish from one net-haul is the minimum and the maximum sizes among all the records of that collection. The average size of the fish from one net-haul is the mean of the means obtained for each record, weighted by the number of specimens it contains.

The weight of the fish (*wt*) was estimated by length-weight power regressions obtained for stomiids caught during the 14th "Challenger" cruise in 1983 (available from G. Swinney, NMSZ) and from material collected during the "Heincke" 135 cruise, 2000 (Chapter 2). The computations of the means of individual stomiid biomass (*avg_wt*) follows the same procedures: the *avg_wt* of the fish from a net-haul is the mean of the means of all records caught by that net-haul, weighted by the number of specimens of each record. The estimated biomass (in g) of stomiids caught by a net-haul is the product of *avg_wt* by the *no_spec* reported for that haul.

The catch-per-unit-effort was defined as the *no_spec* caught per hour of trawling (CPUE n = *fish/h*) and the stomiid biomass caught during the same time period (CPUE wt = *g/h*). The number of stomiid species caught per hour of sampling (*s/h*) was considered a measure of the diversity. Because this ratio depends greatly of the geographical region sampled, another index was calculated: the Longhurst index (%L) relates the catches to the regional diversity. The index is defined as the number of species caught by a net-haul in relation to the total number of species reported for the Longhurst province where it took place.

Gear standard haul computation

Net-hauls were grouped by gear to average cruise and catch data and compute gear specific standard-hauls. Cruise data were described in Chapter 3 and summarised in

Appendix D. A standard-haul catch was characterised by the means, and other basic statistics, of the size-related variables (i.e. *avg_sz*; *min_sz*; *max_sz*; *avg_wt*) and of CPUE n, CPUE wt, *sp/h* and %L. As for a collection, the number of specimens from each record weighted the mean size and weight of the fish sampled by a particular gear. The gear specific features (e.g. mouth area, mesh size) and the sampling methodologies (depth profile, night vs. day hauls, time fishing and towing speed) were regarded as sources of catch variability but those variables were not considered in the analysis. A standard haul catch was interpreted and discussed as the representative sampling "window" of a gear. The histograms of size distribution and the selectivity ogives given in the Appendix D helped the characterization of the catch made by each of the selected gears.

Inter-gear comparisons

The gears were compared in relation to the distribution of the standard-haul catch variables. To smooth those distributions and decrease the weight of the extreme values, the data were transformed by the natural logarithm and standardized. Standardized values were computed as follows: Std. Score = (raw score - mean)/std. deviation. This process allowed ANOVA comparisons between means of the standard haul variables. The probability level of rejection was $p < 0.05$. Since the data are in essence multivariate, a Principal Components Analysis (PCA) was applied to the matrix of standard-hauls. The analysis produced a two-dimensional configuration plot of the samples and permitted an interpretation of the variability expressed along the main axes.

Midwater trawl calibration

The eigenvectors produced by the PCA were used as the coefficients in the linear combinations of variables making up the PC's, for every gear considered. The principal components that explain the variance (in this case the first five PC's) were selected. The value obtained by each gear for each PC was weighted by the percentage that it explains. The score of the gears was computed as the sum of the weighted values of the five PC's. The absolute score distances were scaled in relation to the gear that ranked lower; the reference gear (i.e. the R1m) that assumed a value 1. Then the scores were subject to an exponential transformation and re-scaled in relation to the value 1 of the reference gear. The final net-scores were interpreted as the values that graded the nets according to their selectivity and efficiency to sample the stomiid fauna. Net-scores give the opportunity to compute the fishing effort made by each gear.

Standardised fishing effort

The standardised fishing effort produced by a net-haul was estimated by multiplying fishing time (*t_fishg*) by the net-score. The product was regarded as the standardised hours of fishing (*std_h*). The effort made by an assemblage of net-hauls was computed as the sum of their individual *std_h*. The estimation of fishing effort was extended to net-hauls that were classified only to unspecified commercial (*c_mwt*), micronekton (*m_mwt*) and plankton (*p_mwt*) trawls. The net-scores attributed to those net-hauls were the average of the net-scores obtained for the selected gears classified under the corresponding gear types.

Excluded, were the net-hauls from bottom trawls, those from non-conventional gears and the net-hauls without information on the gear. The missing values of fishing time (*t_fishg*) were filled with the mean *t_fishg* obtained from the net-hauls linked with the same gear or type of gear (see Chapter 2).

Geographical distribution of standardised fishing effort

Because the positions of the net-hauls were known (to varying degrees of accuracy) it was possible to plot the geographical distribution of the fishing effort. Each haul was linked to a 5ºx5º latitude/longitude grid square (*sq_5ºx5º*) and to a Longhurst Provinces (*Lgh_P*). The standard hours of fishing undertaken inside each *sq_5ºx5º* or *Lgh_P* were the sum of the *std_h* of every net-haul linked with that grid square or province.

Results

Catch and gear performances

The basic statistics of the variables that characterize the standard hauls of the twenty gears selected are summarised in the Figure 4.1.

Minimum size. Commercial trawls had high means for *min_sz*; the EMT 1600 clearly attained the highest value (108.4 mm SL). However, the IKMT 10’ DDS, R3m and TT 5’ also missed the smallest individuals in the populations. These three intermediate-size micronekton devices grouped with the EMT 1400, EMT 630-80 and ITGPT in relation this variable (67.8 – 89.3 mm SL). At the other extreme the MOC N1 20 caught the smallest fish (28.2 mm SL). Then the NN, RMT 50, MOC 10 N1, R1.5m, RMT 10, MOC 10, and MOC 20 are grouped in a collection of gears that shared low mean minimum lengths (32.8 – 44.7 mm SL). The RMT 8, IKMT 6’, RMT 8 MC, R2m, IKMT 10’ and R1m are samplers that share the intermediate mean *min_sz* values (44.9 – 61.0 mm SL).

Mean size (*avg_sz*). In general, gears that were unable to catch the small fish also show the highest *avg_sz*. The EMT 1600 and the IYGPT sampled the larger fish (146.8 and 115.9 mm SL, respectively). Then the RMT 50, YFT, EMT 1400, EMT 80-630, TT 5 and the R3m form a cluster of gears that ranked second concerning the variable (89.9 - 112.3 mm SL). The IKMT 10' DDS sampled within the same range. The *avg_sz* of the fish captured by the MOC 20, IKMT 10', RMT 10, RMT 8 MC, MOC 20 N1 and RMT 8 aggregate together and range between 58.5 and 76.5 mm SL. The remaining samplers (R1m, R1.5m, MOC 10, MOC 10 N1 and IKMT 6') grouped around the smaller mean size (from 50.2 to 64.10 mm SL). Only small stomiids (38.1 mm SL) occur at night in surface waters, usually after dusk, where they are caught by the neuston net (nn).

Maximum size. The pattern observed for *max_sz* resembled those reported for the previous variables, showing some variability. The fish sampled by the RMT 50 were by far the largest (217.2mm SL) followed by those from the EMT 1600 and IYGPT (193.0 and 175.3 mm SL). The TT 5 and the R3m clustered together with the remaining commercial trawls (156.7 - 126.5 mm SL). Within the micronekton devices two sub-groups with similar means of *max_sz* were identified: the first included the IKMT 10', IKMT 10' DDS, RMT 8 MC, RMT 10, MOC 20 N1 and MOC 20 (104.8 - 123.9 mm SL); and the second assembled the MOC 10, 10 N1 and the RMT 8, together with the R2m (79.8 – 84.0 mm SL). The R1.5m has an odd position between the last group and that formed by the other plankton trawls (IKMT 6’ and R1m; 55.4 – 67.2 mm SL) and the nn (43.6 mm SL).

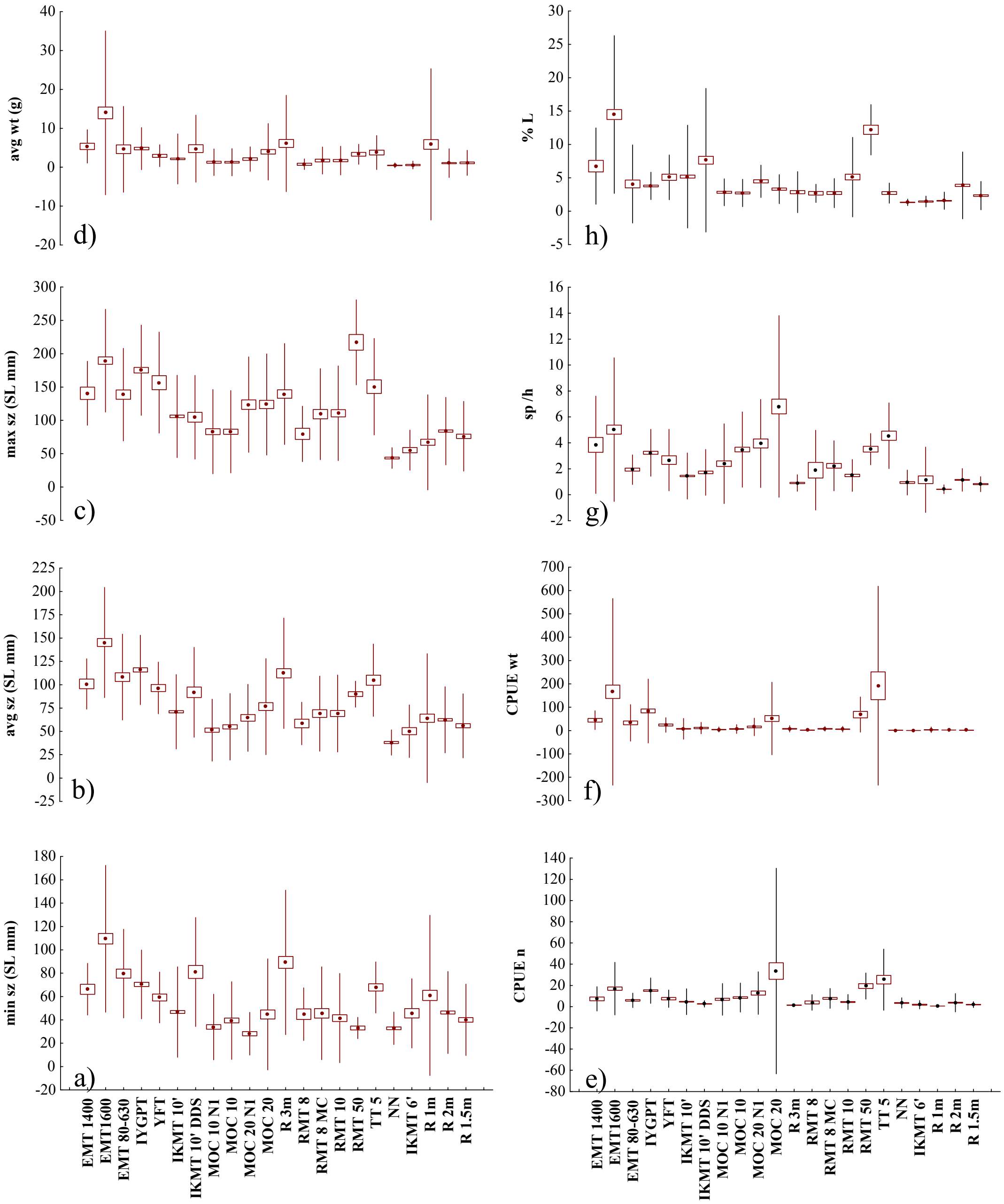


Figure 4.1 Standard-hauls of selected gears. Mean (black dot), standard error (white box) and standard deviation (line). a) minimum size (*min_sz*); b) mean size (*avg_sz*); c) maximum size (*max_sz*); d) mean weight (*avg_wt*); e) capture-per-unit-effort, numbers (CPUE n); f) capture per unit-effort, biomass (CPUE wt) number of species per hour (*sp/h*); Longhurst index (%L). a), b) and c) in mm standard length (SL). See List of Acronyms or Appendix D for gear acronyms.

Mean weight. The estimated mean weight of the fish caught depends of the fish size, of the sample size distribution and taxonomic composition. Since the weight varies exponentially with size in a linear scale the variable is greatly influenced by the larger individuals, which caused some unexpected values. The ln transformed *avg_wt* smoothed the distribution. The estimated average weight of the stomiids caught by the EMT 1600 was the highest (14.0 g). The EMT 1400 and IYGPT shared the second highest means of individual fish weight (5.3 and 4.8 g, respectively). Influenced by the size distribution (several very large individuals), the estimated R1m *avg_wt* reached 5.9g, but statistically the gear ranked lower than the other plankton trawls. The following group integrated the nets that caught relatively large fish and then showed high means of the variable (i.e. R3m, IKMT 10' DDS, TT 5', EMT 80-630, RMT 50, YFT 100; 6.1 - 2.9 g). Again the micronekton trawls split in two groups: the MOC 20, IKMT 10', MOC 20 N1, RMT 8 MC and the RMT 10 (4.0 - 1.7 g); and the MOC 10, MOC 10 N1 and the RMT 8 that clustered with the plankton trawls and neuston net (0.5 to 1.3 g).

CPUE n. Statistically the MOC 20, TT 5', RMT 50 and the IYGPT 100 aggregate together around the highest means of number of fish caught per hour (33.6 - 15.1 fish/h). The MOC 20 N1 ranked slightly below (12.8 fish/h) but clearly above the MOC 10, RMT 8 MC, YFT 100, EMT 1400, EMT 80-630 (8.5 - 5.1 fish/h). The three intermediate-size non-closing micronekton trawls (IKMT 10’, RMT 10 and RMT 8) had approximately the same mean CPUE n (4.7 - 3.9 fish/ h). The IKMT 10’ DSS produced less fish and had a comparable mean to R2m and the neuston net (3.7 - 2.6 fish/h). The R1.5m (1.9 fish/h) and the R3m fished better than the IKMT 6’, which also performed better than the R1m (0.6 fish/ h).

CPUE wt. The biomass caught per hour of trawling is influenced by the number of fish and by the average fish weight. The TT 5’ obtained the highest mean CPUE wt (192.0 g/h) but, due to shape of the size distribution, that value was not considered different from those computed for the RMT 50, IYGPT and even the EMT 1400 (83.9 - 44.3 g/h). The mean CPUE wt for the EMT 1600 (167.6 g/h) was statistically the highest. The MOC 20, YFT and EMT 80-630 (51.5 – 17.7 g/h) sampled less biomass per unit time than the above gears. The group of gears that shared the same statistical CPUE wt mean included the MOC 20 N1, IKMT 10' DDS, R3m and RMT 8 MC (15.7 – 7.6 g/h). Other micronekton nets (IKMT 10', MOC 10 and RMT 10: 7.6 - 5.8 g/ h) rank above the MOC 10 N1 (4.4 g/h) and a group formed by the R2m, RMT 8 and NN (2.2 - 1.6

g/h). The R1.5m (1.6 g/h) and the IKMT 6' (0.5 g/h) caught more biomass of stomiids per hour than the R1m.

Sp/h. The MOC 20 sampled the highest number of stomiid species per net-haul (6.8 sp/h). The other seven gears (EMT 1600, TT 5', MOC 20 N1, EMT 1400, RMT 50, MOC 10 and IYGPT 100) also had high scores for this ratio (3.2 - 4.9 sp/h) and formed a homogeneous group. Next, the test clustered two commercial (YFT and EMT 80-630) with two micronekton nets (MOC 10 N1 and RMT 8 MC), with values ranging from 2.0 to 2.6 sp/h.

Two further groups were identified for the remaining devices: RMT 8, RMT 10 and IKMT 10' (1.4 -1.9 sp/h); and IKMT 6', NN, R1.5m (0.8 - 1.2 sp/h). The R2m, R3m and R1m (1.1, 0.9 and 0.4 sp/h, respectively) did not grouped with any other gear and had some of the lowest values.

L%. An average haul made by the EMT1600 and by the RMT 50 sampled 14.5 % and 12.2 %, respectively of the stomiids species expected to be present. The other four groups with similar mean %L were: IKMT 10' DDS, IKMT 10', RMT 10, YFT, MOC 20 N1 and IYGPT (3.8 - 7.6 %); R2m, MOC 20, EMT 80-630 (3.2 - 3.9 %); R3m, MOC 10 N1, MOC 10, RMT 8 MC, TT 5', RMT 8 (2.8 - 2.7 %); R1m, IKMT 6' and NN (1.3 – 1.6 %).

Spatial comparison between gears

The two-dimensional configuration plot produced by the PCA explains 91.7 % of the variation observed between the selected gears (Fig. 4.2; Table 4.1). As expected from the above comparisons the commercial trawls separate from most of other trawls. A gradient from the EMT 1600 to the EMT 80-630 is apparent. The majority of intermediate-size micronekton devices formed a compact group between commercial and plankton trawls. The exceptions were the small TT 5, the IKMT 10’ DDS and the R3m, that were placed closer to the commercial trawls. The RMT 50 and the MOC 20 (and 20 N1) clearly separated from the remaining devices. The MOC 10 was located closer to MOC 20 than any other micronekton trawl. The plankton trawls grouped together showing a clear gradient between R1m and R2m. The neuston net (nn) associated with the plankton nets.

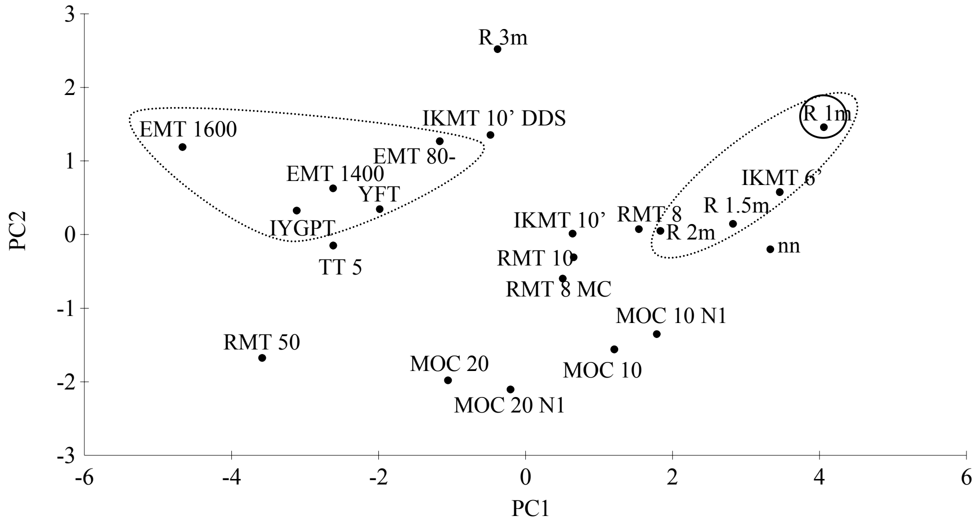


Figure 4.2 Selected gear two dimensions principal component analysis (PCA) of the variables that characterize a standard haul (*min_sz*; *avg_sz*; *max_sz*; *avg_wt*; CPUE n; CPUE wt; *sp/h*; and %L). Dotted lines enclose the devices that belong to commercial midwater trawls (left) and plankton midwater trawls (right). Eigenvalues and eigenvectors are shown in Table 4.1. For acronyms see List of Acronyms or Appendix D

Gear calibration

The eigenvalues, eigenvectors and the net-scores computed are presented in Table 4.1. Commercial and the bigger micronekton trawls obtained the highest net-scores compared with the intermediate-size micronekton and plankton gears. Like the PCA plot, the gradient ranged from EMT 1600 to R1m. The RMT 50 and the IYGPT attained the second and the third highest net-scores, respectively. Resulting from the unexpected standard-haul catch characteristics, the TT 5 attained a dubious fourth position. The MOC 20 ranked among the less efficient commercial trawls (EMT 1400, YFT and EMT 80-630) and together with the MOC 20 N1 scored above any of the other micronekton trawls. The intermediate-size micronekton gears attained net-scores between 7.7 and 4.4 in relation to R1m. Consistently, the non-closing versions (and the net 1 of the MOCNESS tows) ranked lower than the open-closing nets operated on the same basic design. The plankton trawls reached the lowest values, decreasing from R2m to R1m, the net that assumed the reference value. Naturally, the net-hauls classified as unspecified commercial trawls got a higher average score (37.6) than those classified as micronekton (9.1) and plankton (2.1) midwater trawls.

Table 4.1 Principal component analysis (PCA on standard hauls matrix; Fig. 4.2) eingenvalues (A) and eigenvectors (B). C. Relative net scores and estimated total effort in standardised hours of fishing (s*td_h*; i.e. time fishing * net-score) for the selected gears (see Appendix D for acronyms and text for methodological explanations)

A

PC	Eigen values	Var %	Cum Var
1	5.89	73.7	73.7
2	1.44	18	91.7
3	0.45	5.7	97.4
4	0.11	1.3	98.7
5	0.08	0.9	99.6

B

Eigenvectors					
Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Min_sz	-0.238	0.644	-0.31	-0.463	-0.07
Avg_sz	-0.378	0.318	-0.026	0.177	-0.349
Max_sz	-0.399	0.021	0.174	0.543	-0.478
Avg_wt	-0.387	0.239	0.028	0.142	0.594
CPUE n	-0.329	-0.464	-0.278	0.11	0.181
CPUE wt	-0.406	-0.087	-0.105	0.095	0.389
Sp/h	-0.327	-0.429	-0.394	-0.445	-0.329
%L	-0.336	-0.138	0.793	-0.469	-0.003

C

Gear	Net-score	*std_h*
EMT1600	76.7	39193.7
RMT 50	65.4	5379.7
IYGPT	42,7	11824.5
TT 5 *	37.5	232.9*
EMT 1400	30.8	2547.6
YFT	23.5	1775.7
MOC 20	22.4	1645.6
EMT 80-630	14.3	1405.6
MOC 20 N1	14.1	1757.2
IKMT 10' DDS	9.8	3875.4
RMT 8 MC	8.1	1186.7
R3m	7.6	2994.7
MOC 10	6.9	1781.6
RMT 10	6.8	4093.7
IKMT 10'	6.6	20610.1
MOC 10 N1	4.8	1696.4
RMT 8	4.4	219.4
R2m	3.7	6227.4
R1.5m	2.2	1506.9
nn	1.9	955.5
IKMT 6'	1.6	312.6
R1m	1.0	2689.5
c_mwt	37.6	14163,4
m_mwt	9.1	3264,9
p_mwt	2.1	1195,5
mwt	3.6	8148,0

Standardized fishing effort (std_h)

Geographical distribution maps of the net-hauls undertaken by the selected gears are presented in Appendix D. The two gears employed for the major biogeographic studies on Atlantic midwater fish performed 42.5 % of the total sampling effort measured in standard hours of fishing (Table 4.1). The EMT 1600 accounted for a large fraction of that effort, even if the IKMT 10’ undertook about five times more net-hauls than the commercial trawl. Unspecified commercial midwater trawls contributed to 10.1 % of the effort, a number higher than that reached by the IYGPT (8.4 %). Then fourteen devices all together accounted for about a third of the effort. Individually those gears contributed to between 5.8 % and 1 % of the total *std_h* (in decreasing order: R2m; RMT 50; RMT 10; IKMT 10' DDS; R3m; R1m; EMT 1400; MOC 10; YFT; MOC 20 N1; MOC 10 N1; MOC 20; R1.5m; EMT 80-630). As a whole the unspecified plankton trawls, the RMT 8 MC, NN, IKMT 6', TT 5 and RMT 8 accounted for only 2.9 % of *std_h*. The net-hauls classified as unspecified micronekton trawls and other midwater trawls were responsible for 8.1 % of the effort. Due to the exceptional and questionable TT 5 net-score, the *std_h* performed by the device was calculated using the average net-score obtained from all the intermediate-size micronekton trawls.

The sampling effort to produce the 17 771 stomiid occurrences and the 52 554 fish was estimated as 140 684.1 standard hours of fishing (*std_h*) and the net-hauls made by the 20 selected gears represented 81.0 % of that effort.

Geographical distribution of standardized sampling effort (std_h)

The North Atlantic pelagial was unevenly sampled (Fig. 4.3). The region around Bermuda was definitively the most sampled. Other areas that were subject to high fishing pressure include the Gulf Stream region off Nova Scotia, the waters around Madeira, the western Atlantic off USA, the north-eastern Atlantic off the British Isles, and the Mid Atlantic Ridge north of the Azores. In contrast, the central North Atlantic between the meridians 30ºW and 50º W was the region with the lowest incidence of sampling.

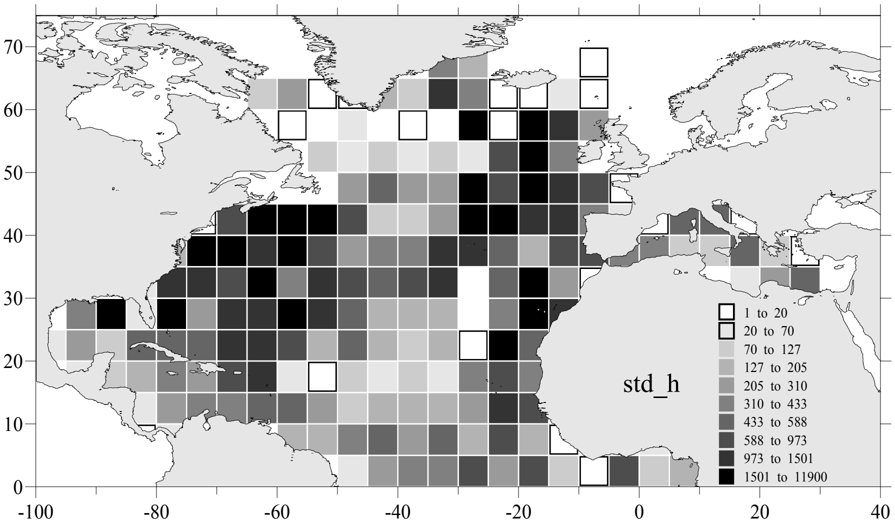


Figure 4.3 Classed (10%) geographical distribution of the estimated midwater fishing effort measured in standard hours of fishing (*std_h*), and distributed in five per five degrees latitude longitude squares (*sp_5ºx5º*). Data from Stomiidae database (*S_db*). See text for explanations.

Considering the distribution of the sampling effort in relation to the Longhurst (1998b) biogeographic system, about 40 % of the total *std_h* occurred inside the GFST and NAST W provinces. NAST E (13.6 %), NADR (12.5 %), NATR (9.4 %) and CARB (9.3 %) were also intensively sampled while ETRA, CNRY, NWCS and BPLR experienced the lower fishing effort (1.4 to 0.6 %). The *std_h* recorded for the remaining provinces ranged from 4.3 % to 2.0 % (in decreasing order: WTRA; ARCT; MEDI and SARC).

Discussion

Catch and gear performances

Commercial trawls

The commercial trawls caught mainly the pre-adult and adult stomiids, missing a high proportion of the smallest and more abundant fish (as reported by Harrisson, 1967; Krefft, 1974; Pearcy, 1980). Post-larvae and juveniles escaped or were extruded through the large meshes of those trawls.

The EMT 1600 caught the larger fish in similar relative numbers to those caught by the IYGPT, which has a net mouth area 6 times smaller. The results show that avoidance by stomiid fishes is negligible in relation to those trawls and thus their catch represented the larger fraction of the stomiid populations. The fish caught by the EMT 1400 were smaller, however this may reflect a geographical effect. The trawl only sampled the gyral subtropical water off Bermuda (Gibbs and Karnella, 1987), where the fish populations are smaller than others under more productive ecological regimes (e.g. Ebeling, 1962; Johnson and Barnett, 1975; Angel, 1997). However, the EMT 80-630 captured fish with similar size to those sampled by the EMT 1400, but in the southern Labrador Sea, Slope Water, and off Newfoundland (McKelvie 1985a,b; McKelvie and Haedrich, 1985), where a large body size stomiiid fauna are expected to occur. However, this trawl was fished mainly during night-time targeting the interzonal micronekton fish that migrate to epipelagic layers, and it is known that large stomiids tend to live on the deeper meso- bathypelagial and reduce the extent of their vertical migration. The EMT 1600 sampled more often the deepest layers than any other commercial trawl. The YGPT was trawled mainly in the upper mesopelagial, but deeper (especially during daytime) than the EMT 80-630. Moreover the young fish trawl was used in the Slope Water regions where the advection of large fishes by warm core rings from the northern periphery of the Sargasso Sea is more evident (Themelis, 1996). There the stomiids were larger than those from most of the southern tropical provinces (Chapters 6 and 7).

The EMT 1600 also attained the highest yields in numbers and biomass per hour of fishing. The lowest CPUEs attained by the EMT 1400 are not clearly explained as both trawls are similar and sampled in a comparable way. Again, the EMT 1400 data were limited in number, space and time and a larger sample would probably show this trawl performing closer to the EMT 1600. The CPUEs achieved by the EMT 80-630 were low perhaps because this trawl was essentially used where the animals that match its selectivity were less abundant (i.e. the epipelagial). Those values were probably also influenced by a biogeographic effect. The IYGPT reached amongst the highest mean CPUEs in a productive region where the stomiid diversity is higher but greatly dominated by a few species. The IYGPT scored the third trawl prior the much larger EMT 1400 and EMT 80-630. Comparatively those seldom used Engel trawls and the YFT fished at lower rates that could be expected. The regular use of the EMT 1600 and IYGPT by the same teams probably improved the *modus operandi* and the way the trawl sampled. The yields in numbers and biomass for the YFT 100 were comparable to those computed for the group of less effective commercial trawls and some intermediate micronekton trawls. This young fish trawl was employed in the vicinity and over the slopes and summits of Mid-Atlantic-Ridge seamounts, where the midwater fish were less abundant (Pusch et al., 2002, 2004). This ecological restriction certainly influenced also the rate the gear sampled regional diversity. The YFT would perform better if the net had sampled only the holopelagial.

The ratio of species per hour of trawling (*sp/h*) correlates better with the CPUE n than with any other variable. This indicates that the more fish caught the highest the probability to sample different species. Indeed the EMT 1600, IYGPT, RMT 50, MOC 20 and MOC 10 got high average numbers of species and specimens per hour. The EMT 1400 was an exception; despite the lower CPUE n attained, its *sp/h* was similar to the above gears. This reflected the success of the trawl in sampling the fauna reported for the NAST W province. The EMT 1400 operated off Bermuda a “hot-spot” of Stomiidae diversity (Beebe and Crane, 1939; Gibbs, 1971; Chapter 7). In contrast the IYGPT fished at a low rate the stomiid species richness reported to occur in the Slope

Water, which may be related with the existence of large numbers of rare stomiid species in that province (Jahn and Backus, 1976; Themelis, 1996; Chapter 7).

Micronekton trawls

Large and very large nets

The RMT 50 was large enough to prevent avoidance by most micronekton fish and had a relatively small mesh size that retained a portion of small fish. Because the net caught a large size spectrum, the computed CPUE's attained were also among the highest means. However, this trawl was operated by Clarke and Pascoe (1985) off Madeira during an experiment that aimed to measure the effect of artificial light on the capture of micronekton. The authors concluded that for most fish species artificial light significantly enhanced the size of the individuals sampled and the yields in numbers and biomass (see also Swinney et al., 1986 and Clarke and Pascoe, 1998). The RMT 50 got the second highest score (Table 4.1), certainly benefiting from the effect of the light on the stomiid captures.

The MOC 20 effectively sampled the smallest fish, but failed to sample a proportion of the larger adults, which presumably were able to avoid the gear. The means obtained for the size-related variables were between those recorded for the commercial (and RMT 50) and intermediate-size micronekton trawls. Resulting from its great ability to catch the smaller and more abundant fish, the MOC 20 reached among the highest CPUE n. The CPUE wt ranked lower because of the small weight of the fish caught. The MOC 20 sampled quite well the regional biodiversity. The nets were towed obliquely at discrete strata of 200-250m, a wide horizon to be shared by several species if some vertical segregation exists. Wiebe et al. (1985) showed the differences between the MOC 20 N1 and the MOC 20 performance (e.g. volume of water filtered per unit time and catch parameters). In this study the N1, in general, captured smaller fish than the MOC 20, but in relation to size variables both nets grouped together and with other multi-closing micronekton samplers. The MOC 20 N1, however, caught fewer fish and less biomass per unit time than the MOC 20, and this may possibly be related with the hypothetical stomiid fish avoidance behaviour (Harrisson, 1967 but also Barkley, 1964 and Clutter and Anraku, 1968).

As expected, because of its characteristics, the MOC 20 ranked between the lower grade commercial trawls and the intermediate micronekton trawls. Craddock et al. (1987,

1992) used this gear to describe the transport of Sargasso Sea midwater fish advected into the Slope Water by warm-core-rings. The hydrographical framework where sampling occurred probably influenced the results obtained.

Intermediate-size nets; open-closing systems

The IKMT 10' DDS inadequately sampled the smallest and the largest stomiids. However, the relative contribution of large fishes influenced the values reached by the size-related variables. Because of its selectivity, the CPUE n obtained for this trawl ranked low within the group of micronekton gears. The scarcity of small fish from its catch probably can be explained by the relatively large mesh size (Table 3.1). The gear was used in the epi- and mesopelagial and avoidance certainly accounted for the low incidence of large fish. The IKMT 10' DDS poorly sampled the stomiid biodiversity, probably reflecting the low CPUE n. Despite these results the net attained an unanticipated high score (Table 4.1). Instead it would be expected an IKMT 10' DDS fishing somehow similarly to the open IKMT 10' and less effectively than the other opening-closing micronekton trawls. The net has a smaller mouth area and has bridles in front of the mouth, which is thought detrimentally to affect its fishing performance. However, some of the above considerations may become invalid because part of the data reported for this trawl were obtained from published information (Badcock, 1970; Bekker et al., 1975) and its quality, especially on fish size (15.8% of the records), is limited.

The RMT 8 MC sampled post-larvae and juvenile stomiids well but not as efficiently as both MOCNESS'. The first gear had a larger mesh size (0.48 vs. 0.3mm) and was towed at higher speed; both factors promoted extrusion of the smallest fish (e.g. Aron and Collard, 1969). Like most of micronekton trawls, the RMT 8 MC sampled the largest fraction of the stomiid populations poorly, because of avoidance. Remarkably the MOC 10 also failed to capture the moderately large individuals and it got low means for fish size comparable to plankton trawls. The reduced incidence of the large size classes may indicate the propensity of the gear to induce fish avoidance. The MOCNESS is characterised by its large and heavy rigid frame (Wiebe et al., 1985) that eventually produce stronger acceleration fronts in front of the net mouth. Those low-frequency vibrations if detected by fish give them a chance to avoid the net as noted by Harrisson (1967) and Clutter and Anraku (1968). This speculation needs to be evaluated.

The RMT 8 MC and the MOC 10 attained a relatively high CPUE n, similar to those computed for the EMT 1400, EMT 80-630 and YFT. Both gears sampled efficiently the fish that match their specific selectivity. However, the small average weight attained produced a relatively lower CPUE wt rank, especially for the MOC 10. Resulting from a high CPUE n the MOC 10 fished quite well in terms of species per hour, at a ratio similar to that reached by commercial and large micronekton trawls. The RMT 8 MC sampled the biodiversity less well, maybe reflecting the geographical context the net was fished. The MOC 10 N1 ranked for most of the variables considered next to the MOC 10; it caught, however, slightly smaller and lighter fish, but within a wider size range. The discrepancies between these identical nets, which sampled distinct depth profiles, were more noticeable in relation to the CPUE n and that may reflect the differences between the filtering performances of both nets as reported for the MOCNESS 20 (Wiebe et al. 1985). Nevertheless the similarity between these two assemblages of net-hauls (as for MOC 20) may be a sign of the accuracy of the approach.

The RMT 8 MC scored amongst the highest within the intermediate-size micronekton trawls. Even knowing this gear is under-represented, the quality of its data is good and the result seems to correspond to its expected relative efficiency. The final net score of the MOC 10 was slightly lower than the RMT 8 and higher than the non-closing micronekton trawls.

The results obtained for the catches made by the small multi-closing TT 5 were the most atypical and unexpected. For a good number of the variables considered it grouped with large commercial trawls and ranked the fourth best gear in sampling the stomiid fauna (Table 4.1)! This doubtful result can possibly be reported to errors associated with biological or cruise data, both at the source or during processing. At the best this trawl would fish as the other intermediate-size micronekton trawls. The material associated with TT 5 should be reviewed. The inclusion of data from the Gulf of Mexico (e.g. Hopkins and Lancraft, 1984, Sutton and Hopkins, 1996a) would improve the accuracy of the analysis.

Intermediate-size nets; non-closing systems

On average, the small fish caught by the IKMT 10’ were larger than those caught by the RMT system (e.g. RMT 8 MC, RMT 8, RMT 10), and especially by both MOCNESS’.

Again this can be interpreted as an effect of escapement and extrusion through the relatively larger net mesh size of that trawl combined with a higher standard trawling speed (see Table 3.1). The mean and maximum size (and weight) of the fish sampled by the net were comparable to those values obtained for other intermediate micronekton gears, except for the MOC 10 and RMT 8. The RMT 8 sampled the fish of intermediate size better; the smallest and the largest fish were under represented. Probably the size spectrum of the sample reflects the depth it sampled, that is the epi- and upper mesopelagial by night. At those depths it targeted the juveniles and young adults which are the main vertical migrant fraction of the populations. The relative paucity of post-larva and young fish (to 30 mm SL), which were the most abundant size class in the RMT 8 MC catch (fitted with similar nets), probably can be explained by natural causes such as the absence of recruits when and where the RMT 8 filtered. The RMT 10 also sampled more efficiently juveniles and small adults. However, the abundant size classes distributed widely along the size axis; that is the RMT 10 tended to sample larger fish compared to both RMT 8 versions, which might be an effect of the larger area of the net opening.

The size selectivity and the sampling depth profile of the IKMT 10’, RMT 8 and RMT 10 influenced their relatively low CPUE n values, compared with the MOCNESS’ and RMT 8 MC. A relative lower efficiency could be expected for the IKMT 10’ since the device has a small opening area and bridles in front of it. However, the net fished through the epi- and mesopelagial all the way across the North Atlantic, while the RMT 10, and especially the RMT 8, sampled across more restricted geographical areas, mainly the upper layers of the water column by night. Those methodological differences may be why the improved and larger RMTs achieved the same CPUE n ratio as the IKMT 10’. These three non-closing systems sampled at the same rate the species present, only better than the plankton and ring trawls.

Probably reflecting its larger mouth area the RMT 10 graded better than the IKMT 10’, and the RMT 8. The RMT 8 would rank better if was used under a different sampling regime. A few RMT 10 net-hauls were made with gear equipped with an electric light to test its influence on the micronekton captures (Clarke and Pascoe, 1985). However, the effect of the experiment was not evaluated in this study but it probably contributed for the relative performance of the net.

Micronekton ring trawl

The R3m was called a “young fish trawl” because of its selectivity (mesh size: 1.2 - 2.4 cm, from cod-end to forenet). As expected the net failed to catch post-larvae and small juvenile stomiids. The mean size and weight of the fish sampled was similar to those collected by three commercial trawls, the RMT 50, IKMT 10’ DDS and TT’5. Fish avoidance was masked by the high means of the size-related variables, which are biased by the inefficiency of the R3m to catch the small fish. Moreover, the net caught the adult fish at a very low rate; its CPUE n ranked at same level as the R2m and R1.5m. Conversely, the CPUE wt reached a value similar to that computed for the IKMT 10’ and RMT 10, influenced by relatively large size of the few fish sampled. The capacity to sample the known diversity was similar to that of the plankton nets.

Neuston net

The 1m diameter neuston sampler produced an atypical catch as only two (*Astronesthes*) stomiid species migrate to the neuston layers by night. The nn caught among the smallest fish, but as they belong to one of the most robust genus of Stomiidae, they were heavier than those caught by the plankton trawls (except the R2m). Obviously, the biodiversity rates are limited by the two existing neustonic species. The major difficulty with interpreting these results is to determine if the catch reflects the net selectivity or the fish that occupies the niche. The neuston net fishing strategy is the mirror of that adopted with the R1m.

Plankton trawls

Isaacs-Kidd midwater trawl 6’

The device caught intermediate size fish because it was inefficient in sampling post-larvae and adults. The small fish were able to escape through the relatively large net meshes, whereas the larger specimens of the populations were able to avoid the gear. The averaged variables that characterised the IKMT 6’ standard-haul ranked amongst the lowest even compared to other plankton trawls (e.g. R2m, R1.5m).

Ring nets

The R2m inadequately sampled the smallest and the largest fish, similar to most of the micronekton and plankton trawls. The R1.5m caught an even narrower range of size classes, which shows that it induced avoidance in smaller fish, comparatively to the R2m. The R2m also sampled better in terms of numbers, biomass and species per hour. These results were expected following the differences in the mouth opening areas (trawls fitted with similar mesh size nets). If both ring nets were fished through similar depth horizons (the R1.5m sampled deeper) the differences between them would probably be more accentuated.

Among all the gears studied the R1m showed the most extreme pattern. It sampled mainly the post-larvae and juvenile fish but it also caught several large and very large individuals, probably reflecting the sampling depth profile. The wide range of the data produced means of the size-related variables clearly biased toward those large fish. As expected, the efficiency of the net ranked among the lowest within the plankton trawls. The data transformation and standardization smoothed the distribution and allowed for the definition of the actual rank of the net.

Regarding the ability to sample stomiid fishes the ring nets arranged according to its diameter. The R2m placed closer to low-score micronekton trawls, whereas the R1.5m performed better than the reference net R1m.

Ranking the sampling gear and standardise fishing effort

The high diversity of pelagic samplers used makes it difficult to quantify the relative abundance of any group of organism based on pooled historical data. The computation of relative net-scores permitted the ranking of the nets according to their (stomiid) sampling efficiency.

The efficiency and selectivity of a pelagic sampler depends of its structure (i.e. size of the gear, mouth opening, basic design, mesh size, type of gauze), of the sampling strategy used (e.g. sampling depth, haul profile, tow speed, tow length, period of the day) and of the behaviour of the organisms to be sampled facing the net.

To compare two samplers by, for example, their captures per unit effort (which in a pelagic sampling context is often measured as the volume of water filtered, assuming a 100% fishing efficiency) is certainly an underestimation of the problem. The sampling effort (and the catches) produced by two net-hauls undertaken by a gear towed at the same speed during the same period of time but fishing at different depths may not be comparable even if the volume of water filtered is the same. Values of CPUE considering the unit of time (hour of fishing) as the unit of effort, are expected to be net-haul specific and reflect the ability of the gear to catch the fauna as well as all the other variables that influence the catch. To sample the epipelagic layers during the sunny hours means that no stomiids are expected to be catch, just because they are not there. In this sense to filter those layers during the day constitutes no fishing effort directed to stomiids. The advantage to compare the nets by means of their catches, without taking into consideration any of their features or the sampling procedures, is because the catches inevitably reflects all those factors, which otherwise are difficult to quantify and compare.

The net-scores computed parallel the spatial variation observed in the PCA plot. The method developed to rank the samplers produced a likely pattern: micronekton trawls were placed between the commercial and plankton trawls. At one extreme the EMT 1600 ranked as the sampler that sampled better the stomiid biotopes. It produced a considerable amount of midwater fish (see ZMH/ ISH entry in Appendix C), including the largest ever reported (Krefft, 1974, 1976). At the other extreme the R1m ranked as the less effective net. This ring performed so “well” (i.e. supported several scientific papers about Bermuda midwater fish; e.g. Beebe, 1932b, 1933a, 1937; Beebe and Crane, 1939) only because it fished exhaustively the lower meso- and bathypelagic layers by day, where many components of this midwater fish family dwell. In this sense, the Bermuda Oceanographic Expedition (1929-31) used the best sampling strategy to sample that fish fauna with an R1m. This net can be considered the most basic device able to sample these fishes and has been used as the baseline to grade all the others gears.

Assuming that the relative position acquired by the gears reflects firstly their opening area, mesh size, and volume of water filtered (which relates towing speed and haul length), the observed variation to the expected pattern might be influenced by the: a) sampling strategy adopted (e.g. depth profile); b) extra equipment used (e.g. electric lights); c) geographical and seasonal distribution of sampling; c) sample size; d) data quality and errors; e) or by the method used to grade the nets.

The surprising relative positions of the TT 5, IKMT 10’ DDS and R3m were greatly influenced by the size-related variables. Clearly, the method used to rank the gears valued the samplers that reached high means for fish size, despite the lower CPUE.

The net-scores can be interpreted as a measure of the effort needed to produce the catch reported (i.e. 76.7 R1m and 9.5 RMT 8 MC net-hauls are needed to produce a catch of a similar rank to that one of an EMT 1600 net-haul) or a relative indication of how good a net sampled compared to the others (i.e. the EMT 1600 fished 76.7 times better than the R1m and 9.5 better than the RMT 8 MC). However, the extent of the differences between the gears compared would be wider, than that shown by the net-scores, if the total fishing stations undertaken within a field program had been included instead only those that caught stomiids. The proportion of net-hauls that sampled stomiids was certainly higher for the more effective samplers and smaller for the plankton ring nets (see below).

Anyway, the results obtained from the scoring method allow the geographical distribution of the standardised fishing effort produced to sample that assemblage of stomiid fishes to be plotted. Chapters 6 and 7 present quantitative biogeographic and biodiversity approaches based on the estimated standardised fishing effort.

The extent of the fishing effort

The Stomiidae database compiles an unknown proportion of the effort undertaken to study the North Atlantic midwater fish fauna (to 2000). The family Stomiidae includes several species (e.g. *Chauliodus* spp and *Stomias* spp) that are abundant and occur regularly in most hauls of their spatial-temporal biotope. It includes also many species that are regionally moderately abundant and a considerable numbers of rare species almost everywhere. Therefore, the occurrence of at least one representative of the stomiids in midwater hauls is a probable event if sampling matches their biotope(s). Indeed they occur in more than 80% of the hauls completed in many midwater cruises (e.g. Atlantis II, Cr. 49, 1969; Atlantis II, Cr. 59, 1970; Atlantis II, Cr. 71, 1972; Atlantis II, Cr. 110, 1981), while for other cruises this proportion is much smaller. Even so, it is expected that the database contains the majority of the sampling programs undertaken, which represented the variety of scientific objectives that guided most of the midwater fish research in the North Atlantic.

Recognised deficiencies of the Stomiidae database are the unavailability of a large amount of the material collected by the former Institute of Oceanographic Sciences along the Northeast Atlantic (see BMNH entry at Appendix B); 2) and that from the South Florida University obtained at the Gulf of Mexico (e.g. Gartner et al., 1987; Sutton and Hopkins, 1996a). Also, the Amsterdam Mid North Atlantic plankton expedition, 1980-83 (van der Spoel, 1981, 1985; van der Spoel and Meerding, 1983) and the CAN-CAP Expeditions (van der Land, 1987) deserve to be assessed. This is also the case for most of the midwater programs completed by institutions from the eastern European countries (see Eastern Europe collections in Appendix B). The incorporation of data from other recent midwater programs in the Irminger Sea (e.g. Magnússon, 1996; Sigurðsson et al., 2002), Bear Seamount (Moore et al., 2001, 2002, 2003b, 2004), and Mid-Atlantic Ridge (Bergstad and Godø, 2003) will certainly improved the knowledge about the micronekton faunas of those regions.

Chapter 5 – Stomiidae: a survey

Why Stomiidae? Systematics, ecological and scientific reasons

Since the description of *Chauliodus sloani* in 1801 the systematics of the stomiid midwater fishes has changed considerably over time. If one wants to approach the biogeography and biodiversity of a biological group, it is important to trace back original data and perceive its taxonomy, diversity and classification; this is the reason to present here the following survey.

The main objective of this work is to investigate the biogeography and biodiversity patterns of Stomiidae in the North Atlantic (Chapters 6 and 7). Except for the genera *Chauliodus* (Ege, 1948; Haffner, 1952) and *Stomias* (Ege, 1934; Gibbs, 1969), there is no satisfactory biogeographic/biodiversity analysis of this group of midwater fish.

The Stomiidae family ranks amongst the most diverse midwater fish in terms of taxonomy, morphology and ecology. Presently, its systematics are thought to be relatively well established at the specific and supra-specific levels, at least according to the species concepts developed for the group (see Gibbs, 1986e). As mentioned this is essential information for a biogeographic/biodiversity approach. Other important characteristics of a taxonomic group for selection as an example for pelagic biogeographic/biodiversity are: 1) to include various relatively abundant species and 2) the availability of a large amount of high quality geographical data. The extent of the geographical distribution of the species to be analysed is also a fundamental subject to considered. If fish taxa are restricted to limited areas or regions, the geographical coverage of such an analysis will be constrained. The Stomiidae species are distributed throughout the North Atlantic oceanic realm, except in the Arctic, including widespread species and many that are restricted, or moderately restricted, to specific regions. This is relevant for the analytical approach since it allows identification of species that characterised specific assemblages.

The stomiids are ancient deep-water fishes (sensu Andriashev, 1953) that are thought to have invaded the deep-sea pelagial from benthic biotopes. They have highly specialised morphological and physiological adaptations (the highest amongst the teleosts) that reflects their long evolutionary history of coping successfully with the environment. The evolutionary factors that lead to these specializations and the ecological significance of each of them are poorly known. Fink (1985) inventoried, described and compared the evolution of the anatomical specializations found throughout the stomiid genera, concluding that the group is monophyletic (see below). Despite Fink's conclusions, the Stomiidae are presently classified into six sub-families to accommodate the observed taxonomic diversity. The high phenotypic diversity of the components of the family is apparent, and this probably fuelled speculative analyses on the emergence and spread of a specific character.

In summary: the biogeography and biodiversity of Stomiidae are poorly understood; its systematics, however, are accepted; it is a typical midwater fish family whose representatives occur frequently in micronekton pelagic hauls; the family shows high taxonomic and phenotypic diversity, and occurs throughout the oceanic realm, extending down to the bathypelagial and into the benthopelagic layers on seamounts, crests and continental slopes; ecologically they are highly specialised predators and as such have a significant impact on the dynamics of pelagic ecosystems; however, their biology (e.g. reproduction, growth and life span) is poorly known.

The order Stomiiformes

This order includes several groups of meso- and bathypelagic fishes of primitive Neoteleosts. They are numerically dominant in the pelagial. They are characterised by (Fink and Weitzman, 1982; Harold and Weitzman, 1996), 1) the arrangement of their photophores, organised in series along the body, 2) the type of their tooth attachments and 3) by a special arrangement of jaws muscles and ligaments.

Goode and Bean (1896) first classified the then "rare" stomiids into Astronesthidae, Stomiatidae, Malacosteidae and Idiacanthidae. Regan (1923), profiting from additional material reviewed the classification of the group that was thought, at that time, to be related to the clupeoids. He recognised five families organized in two groups: Gonostomatidae and Sternoptychidae; and Astronesthidae, Chauliodontidae, Stomiatidae and Malacosteidae. The massive systematics surveys undertaken by Regan and Trewavas (1929, 1930) followed Regan's scheme. But just a few years previously, Parr (1927) had created the order Isospondyli, dividing it into 3 sub-orders: Gymnophotodermi (Astronesthidae, Melanostomiatidae and Idiacanthidae [the later included later in Melanostomiatidae; Parr, 1930]); Lepidophotodermi (Stomiatidae and Chauliodontidae); and Heterophotodermi (Gonostomatidae and Sternoptychidae). The

Stomiatidae included *Stomias* and *Macrostomias* (Parr, 1930) and the Malacosteidae were fitted in Melanostomiatidae. But, Beebe (1934) found enough evidence to once again separate *Idiacanthus* from the Melanostomiatidae of Parr (1927, 1930) and from the Stomiatidae of Regan (1923), and hence revalidated the family Idiacanthidae. Beebe and Crane (1939) recombined the two classifications restoring the Malacosteidae family from the Melanostomiatidae, leaving the Stomiatidae with just two genera. Beebe and Crane (1939) discussed the phylogeny of the group and the functional interrelationships among the genera of these families (see comments by Fink, 1985 about their system). Beebe and Crane's classification of the stomiids at the family level prevailed for many decades.

Later, the stomiiforms were re-classified as belonging to the order Salmoniformes (Isospondyli, Protocanthopterygians) and sub-order Stomiatoidei (Greenwood et al., 1966). In the following year, Weitzman (1967a) published a comparative osteological survey of the stomioids, also including them within the salmoniform fishes. Finally, Rosen (1973) revaluated the group and created the order Stomiatiformes, included in the Neoteleostei and considered a sister group of the Eurypterygii. The phylogenetic basal relationships of the Stomiiformes were confirmed by genome technologies (Miya et al., 2001).

Weitzman (1974) proposed a new classification at the sub-order level and recognised two Stomiiformes lineages: the Gonostomata (Gonostomatidae and Sternoptychidae) and the Photichthya, which included the newly erected family Photichthyidae (or Phosichthyidae) and the six families of the advanced Stomiiformes, grouped in the supra-family Stomiatoidea. Steyskal (1980) altered the name from Stomiatiformes, Stomiatidae and Melanostomiatidae to Stomiiformes, Stomiidae and Melanostomiidae. Fink and Weitzman (1982) established the monophyly of the Stomiiformes, based in several characters, such as the peculiar structure of their photophores and tooth attachments. Fink (1984) summarized his main conclusions about the phylogeny of the stomiid fishes. These then were published in greater detail later (Fink, 1985). He accepted the sub-order lineages of Weitzman (1974), but did not recognise the validity of the families under the Stomiatoidea, and established a unified Stomiidae family (Fink, 1984, 1985). Nelson (1994) accepted the composition of the sub-orders as defined by Weitzman (1974) but uses a different nomenclature: Gonostomatoidei and Photichthyoidei. Harold and Weitzman (1996) in their review of the phylogeny of the

Stomiiformes corroborated the classification (and the nomenclature) established previously (Weitzman, 1974; Fink, 1984, 1985), however, suggested a need for further research.

The Family Stomiidae

Fink (1984, 1985) grouped the former Astronesthidae, Stomiidae, Chauliodontidae, Melanostomiidae, Idiacanthidae and Malacosteidae within a single family: the Stomiidae. The author based his phylogenetic study on a cladistic approach involving 330 characters (skeleton, head muscles, photophores, and other parts of the soft anatomy), and suggested the monophyly of the group, based on 17 characters, relegating the supra-family Stomiatoidea to the family level. Fink considered his scheme as an expansion of the Stomiatidae of Regan (1923) and Regan and Trewavas (1930). He produced a cladogram of the genera included in the new family and discussed the relationships among "sister-groups" (Fig. 5.1).

The classification of Fink (1985) was not immediately accepted: for example in the Smith's Sea Fishes (Smith and Heemstra, 1986) and the Checklist of the Fishes of the Eastern Tropical Atlantic (CLOFETA; Quéro et al., 1990) the authors continue to use Beebe's family classification (followed by Morrow and Gibbs in the Fishes of the Western North Atlantic; Bigelow et al., 1964). The system is still in use by some authors (e.g. McEachran, and Fechhelm, 1998). However, in his last edition Nelson (1994) agreed to the unified Stomiidae of Fink (1985) but the author retained "…some elements of the former classification to avoid making major changes that may themselves be short-lived". Nelson (1994) arranged the stomiids in five sub-families and two tribes: Astronesthinae; Stomiinae (Tribe: Stomiini and Chauliodontini); Melanostomiinae; Malacosteinae; and Idiacanthinae. Eschemeyer (1998) recognised Fink's (1985) Stomiidae but also retained the infra family classification of Nelson (1984), and placed Stomiini and Chauliodontini into sub-family category (Chauliodontinae and Stomiinae).

The fossils of Stomiidae

The stomiids are considered to be an ancient (primary) group of deep-sea pelagic animals (Andriashev, 1953). Fossils of several stomiiformes occurred in the middle-Miocene deposits, at a time when the geographic distribution of the marine biota, and marine temperatures profiles were very similar to the patterns observed today (Marshall, 1963). Parin (1984) presented some theoretical considerations supporting the idea that mesopelagic fish fauna evolved from benthopelagic and/or mesobenthic ancestral forms living in the benthopelagial. The phylogenetic origin of the Stomiiformes was further studied and discussed by Weitzman (1967a): ancient members of the group were identified and compared to fish from other orders considered less derived. The fossils ascribed to the Stomiiformes were analysed but none were considered direct ancestors of the stomiids. Fink (1985; Appendix II) reviewed the (five) available fossil fishes attributed to the Stomiidae and considered only two of them to be members of the group. One of those, found at the Eocene sediments of Georgia, was considered a probable species of the genus *Astronesthes* (*A. praevius*). The other was a fossil named *Chauliodus eximius* (Jordan, 1925) and dated from the middle-Miocene sediments at the southern California. The species has been re-examined by Crane (1966) who supported a “phylogenetic” biogeographic analyses of the evolutionary history of the viperfishes

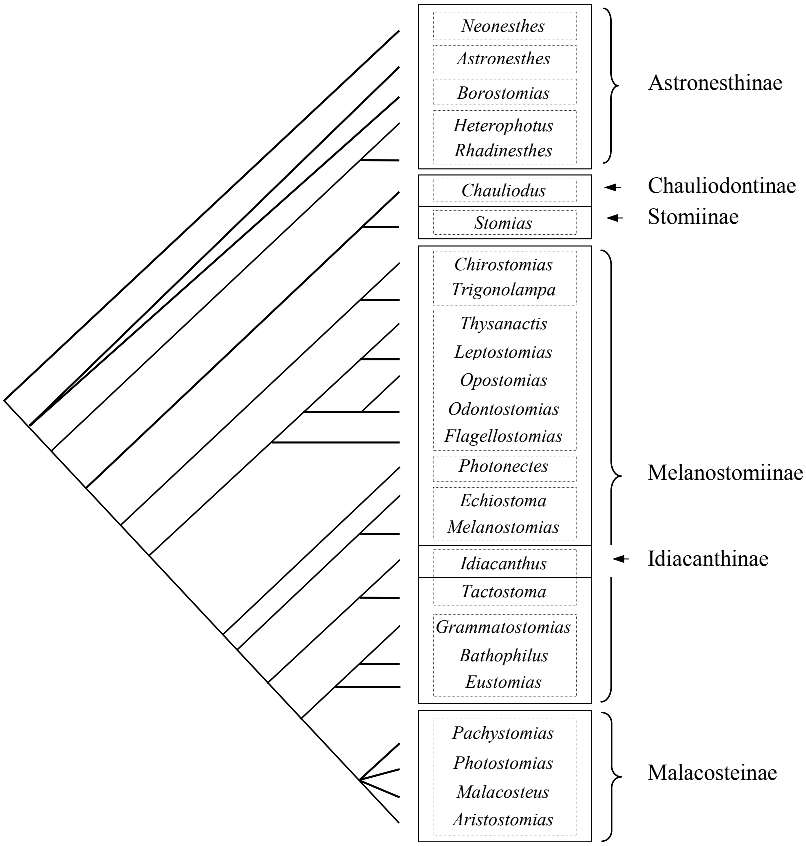


Figure 5.1. Cladogram of the phylogenetic interrelationships among stomiid genera (redraw after Fink, 1985). Solid line boxes: genera from the same sub-family; dashed line boxes: genera from the same clade.

species. Parin and Novikova (1974) critically reviewed Crane's (1966) study and only partially agreed with the proposed scheme. A new stomiiform genus from the middle-Eocene sediments of Georgia has recently been described (Prokofiev, 2000). However, palaeontological evidence to support any ideas concerning the long evolutionary history of the Stomiidae remains very scarce.

Basic bibliography on Stomiidae genera and species

There are several relevant reviews concerning the systematics of North Atlantic stomiid genera and species: the Fishes of the Western North Atlantic (FWNA: Gibbs, 1964a,b; Morrow, 1964b-d; Morrow and Gibbs, 1964); the Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean (CLOFNAM: Gibbs and Morrow, 1973; Morrow, 1973a,b,c; Krueger, 1973; Goodyear, 1973); the Fishes of the North-eastern Atlantic and the Mediterranean (FNAM: Gibbs, 1984a-e); the Check-list of the Fishes of the Eastern Tropical Atlantic (CLOFETA: Gibbs, 1990a,b; Parin, 1990; Gibbs and Barnett, 1990; Krueger, 1990; Goodyear, 1990). These important publications on regional faunas present primary data on authorities, holotypes, references and synonyms (FWNA; CLOFNAM; CLOFETA), dichotomous keys (FWNA; FNAM), morphological descriptions of adults and other developmental stages (FWNA; FNAM), maximum size, regional and broad geographical distributions, habitat, etc. Although the Smith Sea Fishes (Smith and Heemstra, 1986) considers only the species from around South Africa, most of the keys presented also include species that occur elsewhere in the North Atlantic too and are therefore useful.

Other important publications are the former treatises that shaped the family: Parr (1927), Regan and Trewavas (1929, 1930) and Beebe and Crane (1939). The authors studied the systematics of genera and species based on meristics and morphometrics; described new species; produced keys for their identification; discussed the phylogeny of the group, based on external morphology; revealed peculiar anatomical details of some groups; produced profuse scientific illustrations; gave broad geographical distribution; cruise data, etc.

Obviously, since the first systematics revisions of the group, stomiid classification has changed and most of the keys produced are no longer valid. Currently valid taxonomic keys for North Atlantic species (by genus) are listed in Table 5.1. McEachran and Fechhelm (1998) combined and adapted keys from different authors and produced a key to identify stomiid species reported for the Gulf of Mexico at the family (sub-families) level. Additional contributions on species and genus systematics are referred to below.

Sub-families and genera of Stomiidae

Although the stomiids are classified at the family level in many taxonomic reviews (see below), the keys used to identify the former families are obviously valid for sub-families (i.e. Morrow, 1964a; Weitzman, 1986; among others). References are given in a single block at the end of each section.

Eschmeyer (1998) recorded 62 nominal Stomiidae genera only 26 of which are presently accepted as valid (Fink, 1984, 1985; Nelson, 1994; Harold and Weitzman, 1996; Table 5.1). These genera were described between 1801 and 1939, but the rate of description peaked between 1877 and 1930. The genus Parabathophilus Matallanas, 1984 was synonymised later with Bathophilus by Gibbs and Barnet (1990), but was considered valid by Nelson (1994). The validity of Eupogonesthes, the genus most recently erected by Parin and Borodulina (1993) while describing a new species (E. xenicus) from the Indian Ocean, needs confirmation, as only the holotype is known. No dichotomous key is available to split all the recognised genera.

The phylogenetic tree of Fink (1985) summarizes the interrelationships among the stomiid genera (Fig. 5.1). Several of the sub-clades identified by Fink's analysis had been detected previously (by Parr, [1927], Regan and Trewavas [1930] and/ or Beebe and Crane [1939]), but others were newly identified. A comparative discussion about the results obtained by the different contributions is beyond the scope of this work, only the phylogeny produced by Fink (1985) has been used and summarised here. It is worth noting that the cladogram shows an evolutionary gradient that accommodates quite well the sub-familial classification.

Astronesthinae

This sub-family is at the base of the evolutionary lineage of the stomiids. The osteology and the relationships between the genera of these fishes were detailed and discussed by Weitzman, 1967b. Fink's (1985) results corroborate these observations. The sub-family

Table 5.1 Valid Stomiidae fish genera. Sp.: total number of species recognised at the present; N. Atl: number of North Atlantic species; %: percentage of North Atlantic species in relation to total number of species; Keys to N.Atl sp.: references with keys to North Atlantic species.

Genus	**Authority**	**Sp.**	**N. Atl**	**%**	**Keys to N.Atl sp.**
Neonesthes	Regan & Trewavas, 1929	2	1	50	Gibbs, 1986c
Astronesthes	Richardson, 1845	47	12	25.5	Borodulina, 1992; Parin & Borodulina, 1996, 1997b, 1998b, 2000, 2002
Borostomias	Regan, 1908	5	3	60	Gibbs, 1964a; Gibbs, 1984a
Heterophotus	Regan & Trewavas, 1929	1	1	100	
Rhadinesthes	Regan & Trewavas, 1929	1	1	100	
Stomias	Cuvier, 1816	11	5	45.5	Gibbs, 1969
Chauliodus	Bloch & Schneider, 1801	8	3	37.5	Morrow, 1961; Morrow, 1964a; Parin & Novikova, 1974
Trigonolampa	Regan & Trewavas, 1929	1	1	100	
Chirostomias	Regan & Trewavas, 1930	1	1	100	
Opostomias	Günther, 1887	2	0	0	
Odontostomias *	Norman, 1930	2	2	100	
Thysanactis	Regan & Trewavas, 1929	1	1	100	
Leptostomias *	Gilbert, 1905	12	9	75	Morrow & Gibbs, 1964
Flagellostomias	Parr, 1927	1	1	100	
Photonectes *	Günther, 1887	12	10	83,3	Morrow & Gibbs, 1964;
Melanostomias *	Brauer, 1902	13	8	61.5	
Echiostoma	Lowe, 1843	1	1	100	
Tactostoma	Bolin, 1939	1	0	0	
Idiacanthus	Peters, 1877	4	1	25	
Eustomias	Vaillant, 1888	113	60	53.1	Gibbs et al., 1983; Gomon & Gibbs, 1985; Clarke, 1998, 1999, 2000
Grammatostomias	Goode & Bean, 1896	3	3	100	Morrow, 1959; Morrow & Gibbs, 1964;
Bathophilus	Giglioli, 1882	18	9	50	Barnett & Gibbs, 1968
Pachystomias	Günther, 1887	1	1	100	
Photostomias	Collett, 1889	1	1	100	
Malacosteus	Ayres, 1848	1	1	100	
Aristostomias	Zugmayer, 1913	6	5	83.3	Goodyear, 1980; Gibbs, 1984e
Total		269	141	52.4	

includes five genera: *Astronesthes*, *Borostomias*, *Heterophotus*; *Neonesthes*; and *Radinesthes*. According to Fink (1985) *Neonesthes* is the sister group of all the other genera. The relationships between *Astronesthes* and *Borostomias* are an unresolved trichotomy, but these genera were considered less derived than the sister taxa *Radinesthes* and *Heterophotus*.

References: Brauer, 1902 (species descriptions; meristics and morphometry); Parr, 1927; Regan and Trewavas, 1929; Norman, 1930 (species descriptions; references; synonyms; cruise data); Koefoed, 1956 (species descriptions; references; synonyms; cruise data); Weitzman, 1967b (osteology, morphology, phylogeny); Goodyear and Gibbs, 1970 (*Astronesthes*: systematics; synonyms and references; species diagnosis; meristics and morphometry; vertical distribution; zoogeography); Borodulina, 1994 (*Astronesthes*: systematics; morphology; sexual dimorphism); see also Table 5.1.
Other on non North Atlantic *Astronesthes* species: Gibbs and Amaoka, 1984 (also *A. similis*); Gibbs and McKinney, 1988; Borodulina, 1992; Parin and Borodulina, 1995, 1997a, 1998a, 2001; Parin et al., 1999;

Stomiinae

Stomiinae comprises a unique genus since *Macrostomias* Brauer, 1902 was relegated to a synonym of *Stomias* (Fink, 1985). This conclusion has been corroborated by the phylogenetic studies of Fink and Fink (1986) on *Stomias*, and then it has been accepted by most authors (e.g. Gibbs, 1990a). The cladistic analysis revealed a monophyletic group formed by the eleven recognised species. The scheme of Fink and Fink (1986) supported some of the most relevant approaches to evolutionary pelagic biogeography (White, 1994; Johnson and Zhuaranec, 1998).

References: Brauer, 1906 (systematics; species descriptions; meristics and morphometry); Ege, 1918 (species description and comparisons; larvae and other development stages; vertical distribution; geographical distribution; size data; cruise data); Parr, 1930 (family systematics); Parr, 1931 (species key; many not actually valid); Ege, 1934 (species and sub-species taxonomy; meristics and morphometry; geographical distribution; phenotypic variability; vertical distribution; zoogeography; cruise data); Shcherbachev and Novikova, 1976 (systematics; species lists; species key; meristics and morphometry; geographical distribution); Fink and Fink, 1986 (species phylogeny; cladistics; anatomical descriptions).

Chauliodontinae

Similar to the previous sub-family, the Chauliodontinae also includes only one genus: *Chauliodus*. *C. sloani* was the first stomiid to be described about 200 years ago. Several authors (Morrow, 1961; Crane, 1966; Parin and Novikova, 1974) attempted to disentangled the phylogeny of the *Chauliodus* species. However, none of those studies seems completely acceptable since they were based mostly on external morphology and, as Parin and Novikova (1974) stated, it is problematic to resolve adequately the evolutionary trends in a compact and poorly differentiated group such as the genus *Chauliodus*.

Stomias is a sister genus of *Chauliodus* and both form a sister group of all the remaining stomiids, except the Astronesthinae. According to Fink (1985) numerous morphological features are shared by the two genera (e.g. the nasal bones; the palatine tooth into two groups; the bifurcated branchiostegals; and the hexagonal pigmentation of the skin, among other characters), which better justify the resulting clade. These similarities may have weighted Nelson's (1994) decision to accommodate both genera in two tribes belonging within the Stomiinae sub-family. However, for precaution the classification of Eschmeyer (1998) was adopted.

References: Regan and Trewavas, 1929; Ege, 1948 (species and sub-species taxonomy; meristics and morphometry; geographical distribution; phenotypic variability; vertical distribution; zoogeography; cruise data); Haffner, 1952 (morphology; vertical distribution; biogeography); Tchernavin, 1953 (functional morphology; feeding behaviour); Morrow, 1961 (systematics; synonyms; references; species description; key to species; meristics and morphometry); Crane, 1966 (systematics; interrelationships; fossils); Parin and Novikova, 1974 (species descriptions; key to species; synonyms and references; meristics and morphometry; functional morphology; phylogenetic approach on species interrelationships; occurrence data; geographical distribution; geographical variability; cruise data);

Melanostomiinae

This monophyletic group was created by Parr (1927) to include the fishes extracted from Regan's (1923; and Regan and Trewavas, 1930) Stomiatidae. The melanostomiids show the highest generic and specific diversity (see Table 5.1). The sub-family comprises six clades including 14 genera which are intermediate between the less derived sub-families and the clade that includes the Malacosteinae. *Idiacanthus,* a sister genus of *Tactostoma*, was classified among the Melanostomiinae, which seems to reflect the previous uncertainty about its actual relationships (see above).

Chirostomias and *Trigonolampa* (both monotypic) are the basic melanostomiid genera. The following clade includes five genera: *Flagellostomias*; the sister genus *Leptostomias* plus *Thysanactis*, and *Odontostomias* plus *Opostomias*. The peculiarities and the diversity of characters shown by *Photonectes* placed the genus as a sister group of the most derived stomiids. The following clade includes three sub-groups: *Melanostomias* and *Echiostoma*; *Idiacanthus* and *Tactostoma*; *Eustomias* and *Grammatostomias* plus *Bathophilus.*

References: Brauer, 1902 (species descriptions; meristics and morphometry); Welsh, 1923 (systematics; species descriptions; meristics and morphometry); Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane (1939); Norman, 1930 (species descriptions; references; synonyms; cruise data); Beebe, 1932c (species descriptions; meristics and morphometry); Beebe

1933a (species descriptions; meristics and morphometry); Morrow, 1959 (*Grammatostomias*: species description; meristics and morphometry; key to species); Gibbs, 1971 (*Eustomias*: species description; species composition; seasonality; vertical distribution); Parin and Pokhilskaya, 1974 (*Eustomias*: mainly Indo-Pacific, also Atlantic; systematics; species lists; species key; species meristics and morphometry; phylogenetic approach; geographical distribution; cruise data); Parin and Sokolovsky, 1976 (Pacific; species descriptions; meristics and morphometry; geographical distribution); Parin and Pokhilskaya, 1978 (*Melanostomias*: species lists; species key; species meristics and morphometry; geographical distribution). See also Table 5.1.

Idiacanthinae

The dragon fishes of the genus *Idiacanthus* have a peculiar external morphology that led Beebe (1934) to place them in a separate family. However, Fink's (1985) analysis using only the adult characters of the females placed the group among the melanostomiids. The paedomorphic males and the larvae with stalked eyes, among other features, may justify the adoption of Idiacanthinae. This was corroborated by the review of Kawaguchi and Moser (1984) on the stomiids larval forms.

References: Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933b (systematics; morphology larvae, females and males); Beebe, 1934 (systematics; development; anatomy; morphology; sexual dimorphism; seasonality; reproduction); Novikova, 1967 (systematics; species descriptions; meristics and morphometrics; geographical distribution; cruise data);

Malacosteinae

The group includes fishes that have acquired the most derived characters within the family. Goodyear (1980) presented the fullest systematics survey on the malacosteids (included a phylogenetic [cladistic] approach), but his results were never published in the literature. Historically, only the *Photostomias*, *Malacosteus* and *Aristostomias* have been considered to be members of the "losejaws". However, Goodyear (1980) included *Pachystomias* within the "Malacosteid-grade", a decision corroborated by Fink (1985). The analyses of Goodyear (1980) and Fink (1985) were less conclusive about the interrelationships within the clade resulting in an unresolved polychotomy. *Malacosteus* and *Pachystomias* are monotypic, whereas *Aristostomias* includes several recognised species. At the present the systematics of the genus *Photostomias* is being investigated (see below).

References: Regan and Trewavas, 1930; Beebe 1933a (species descriptions; meristics and morphometry); Goodyear, 1980 (systematics; species descriptions; species diagnoses; synonyms; references; phylogeny; geographical distribution; occurrence data).

Sub-generic taxa of Stomiidae

Sub-generic, or supra-specific taxa, group species within the same genus that share several characteristics though of systematics (or at the best phylogenetic) significance. When structuring their classification system, Regan and Trewavas (1930) erected several sub-genera to accommodate the variability observed within the highly specious genera (i.e. *Photonectes*, *Eustomias* and *Bathophilus*). Recently the concept of species-group, a category that lies between the sub-genus and the species, was adopted to include some closely related taxa, namely among the *Astronesthes* and *Eustomias*.

Photonectes

The high diversity in *Photonectes* led Parr (1927) and Regan and Trewavas (1930) to sub-divided the genus into two or five sub-genera, respectively. These were: *Melanonectes* Regan and Trewavas, 1930; *Photonectes* Günther, 1887; *Dolichostomias* Parr, 1927; *Microchirichthys* Regan and Trewavas, 1930; and *Trachinostomias* Parr, 1927. The last two have the dorsal and anal fins covered with thick black skin, a characteristic that differentiates them from the two remaining sub-genera. Apart from that they also have more serial photophores and differ from the other groups by the number (and structure) of pectoral fin rays. The closely related and "most primitive" sub-genera *Melanonectes* and *Photonectes* differ in the number of pectoral fin rays (two in the first group and none in the second) and in the arrangement of the serial photophores. *Dolichostomias* are slender species with a peculiar organization of the fins.

Beebe and Crane (1939) rejected this classification of Regan and Trewavas (1930) and reduced the *Photonectes* to only two sub-genera, closely following Parr (1927). Finally, Morrow and Gibbs (1964) once again regrouped the *Photonectes* according to Regan and Trewavas (1930), but included the *Microchirichthys* into the *Trachinostomias*, as they observed a minute second pectoral fin ray in *P. margarita* (which was the only valid species of *Microchirichthys*). The high morphological diversity of the group was observed by Fink (1985), who remarked "… some trenchant osteological differences even among specimens recognised on standard external characters as conspecific". The author also stated that "… an understanding of this genus is barely sketched out at this point".

Bathophilus

Six sub-genera of *Bathophilus* were established without comments by Regan and Trewavas (1930) and corroborated by Morrow and Gibbs (1964): *Notopodichthys*, *Bathophilus*, *Trichostomias*, *Gnathostomias*, *Trichochirus*, and *Dactylostomias*.

The definitions of these sub-genera are related to the insertion position, organization and numbers of pectoral fin rays. However, the system was not accepted by Barnett and Gibbs (1968) and since nobody else has referred to it. The authors do not "… recognise the pectoral rays … as being in two groups in some species, as opposed a single group in others", which indicates the inconsistency of the sub-genus *Trichostomias*, and probably of the whole system. Moreover, it seems that a classification based solely on numbers and arrangements of pectoral fin rays hardly reflects the phylogenetic interrelationships between the *Bathophilus* species. Therefore the sub-genera of *Bathophilus* have not been considered phylogentically relevant.

Eustomias

Regan and Trewavas (1930) again proposed the subdivision of *Eustomias* into supra-specific taxa. They fitted their 52 species into 10 sub-genera according to the structure of the barbel, the number of rays in the pair fins, and the nature of dentition. The taxa then erected were: *Spilostomias*; *Urostomias*, *Haploclonus*; *Eustomias*; *Nominostomias*; *Rhynchostomias*; *Achirostomias*; *Triclonostomias*; *Dinematochirus*; and *Neostomias*. Gibbs and Morrow (1964) in rejecting this system considered it too artificial to be useful. Parin and Pokhilskaya (1974), while discussing the sub-generic structure defined previously, created their own system organizing the *Eustomias* in lineages and sub-groups. Later, Gibbs et al. (1983), profiting from greater number of specimens, pointed out the value of the sub-genera defined by Regan and Trewavas (1930) and reviewed and re-organised the classification. The authors suggested the following major modifications: to include *Urostomias* within *Spilostomias*; exclude the 2-rayed species from *Nominostomias*; and combine the *Achirostomias* with the *Dinematochirus*. Gibbs et al. (1983) reviewed the *Nominostomias* species and Gomon and Gibbs (1985) created the sub-genus *Biradiostomias* to accommodate the species with two pectoral fin rays extracted from the former group. Clarke (1998, 1999, 2000, 2001) reviewed the species included in *Dinematochirus*. Gibbs et al. (1983) assigned *E. lipochirus* to *Dinematochirus* but Clarke (1998) stated that the form has a simpler barbel compared to the others members of the group and did not treated the species. This may imply the recognition of the *Achirostomias* to accommodate the species. Fink (1985) has commented on the complex sub-generic organization of the *Eustomias*, and considered the attempts made "…largely unsuccessful because there have been no explicitly phylogenetic analyses, and characters purporting to diagnose most groups are usually combination of primitive and derived traits". The statement was already recognised by Gibbs et al. (1983) that referred the need for "… more work … before this scheme can be examined in a phylogenetic context". However, the authors expected that the sub-genera would be found to be monophyletic.

Species groups

Groups of species were created within *Nominostomias* and *Biradiostomias* (Gibbs et al., 1983; Gomon and Gibbs, 1985). In the first paper no references were made about the five groups considered; however, in the second paper the authors mentioned that the groups were created for convenience in the discussion and that they "…may or may not reflect phylogenetic categories." The groups (as the sub-genera) were created according to the structure of the barbel.

Clarke (1998, 1999, 2000, 2001) did not assumed any taxonomic status for the groups of *Dinematochirus* treated. However, in the former two contributions he reviewed and described species "associated" to *E. achirus* and "similar" to *E. dendriticus*, based again on the complexity and structure of the barbels.

The recent revisions of the genus *Astronesthes* (e.g. Parin and Borodulina, 1996, 1998b, 2002) described twenty-two new species and seven species-groups. Most of the *Astronesthes* were fitted within those groups that were named after a "typical" species (e.g. *A. indicus*; *A. cyaneus*; and *A. niger*). Other six species, considered rare and poorly known (Parin and Borodulina, 2000) were not included in any of the groups considered.

Specific composition of Stomiidae genera

Twenty-six Stomiidae genera are recognised today as valid (Eschmeyer, 1998; 27 if *Eupogonesthes* is considered; Table 5.1). The number of species, however, is difficult to estimate, as the systematics of some genera still needs to be reviewed (see below). Nelson (1994) stated that there are 228 valid species, but many new species have been described thereafter. The current total of 269 species computed in this study (Table 5.1) should be regarded as provisional.

The species richness varies considerably among the stomiid genera (Fig. 5.2).

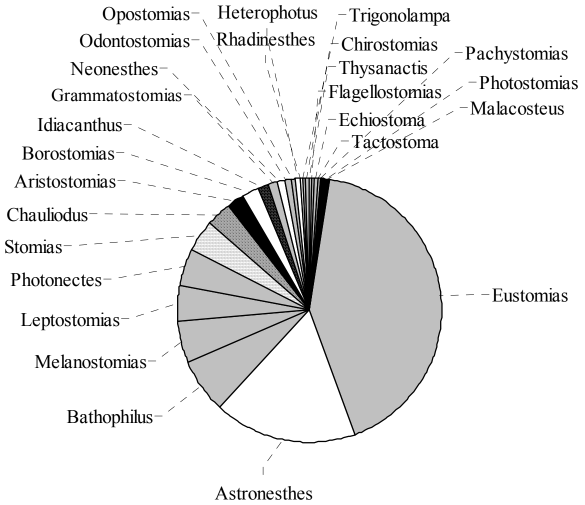


Figure 5.2 Relative species richness (percentage) per Stomiidae genera (for absolute values see Table 5.1). Patterns of the sectors represent the sub-families: Astronesthinae (white); Stomiinae (light dotted); Chauliodontinae (intermediate dotted); Melanostomiinae (grey) Idiacanthinae (heavy dotted); Malacosteinae (black)

Eustomias by far is the most speciose genus and includes more than 40% of all species recognised. These peculiar fishes have been studied intensively at a worldwide scale and, as mentioned, the sub-genera have been created to accommodate its rich diversity. *Nominostomias* is the most diverse sub-genus of *Eustomias*, followed by the *Dinematochirus* and the *Biradiostomias*. In the North Atlantic, however, *Nominostomias* has fewer representatives than the two other groups (Fig. 5.3). *Astronesthes* is the second most speciose genus (47 species). The other genera form a gradient from *Bathophilus* (with 18 species) to *Neonesthes*, *Opostomias* and *Odontostomias*, with two species each, and to twelve (46%) genera currently considered to be monospecific. In terms of sub-families specific composition the melanostomiids, that includes more than 50% of the genera, accounts for 67% of the species. The

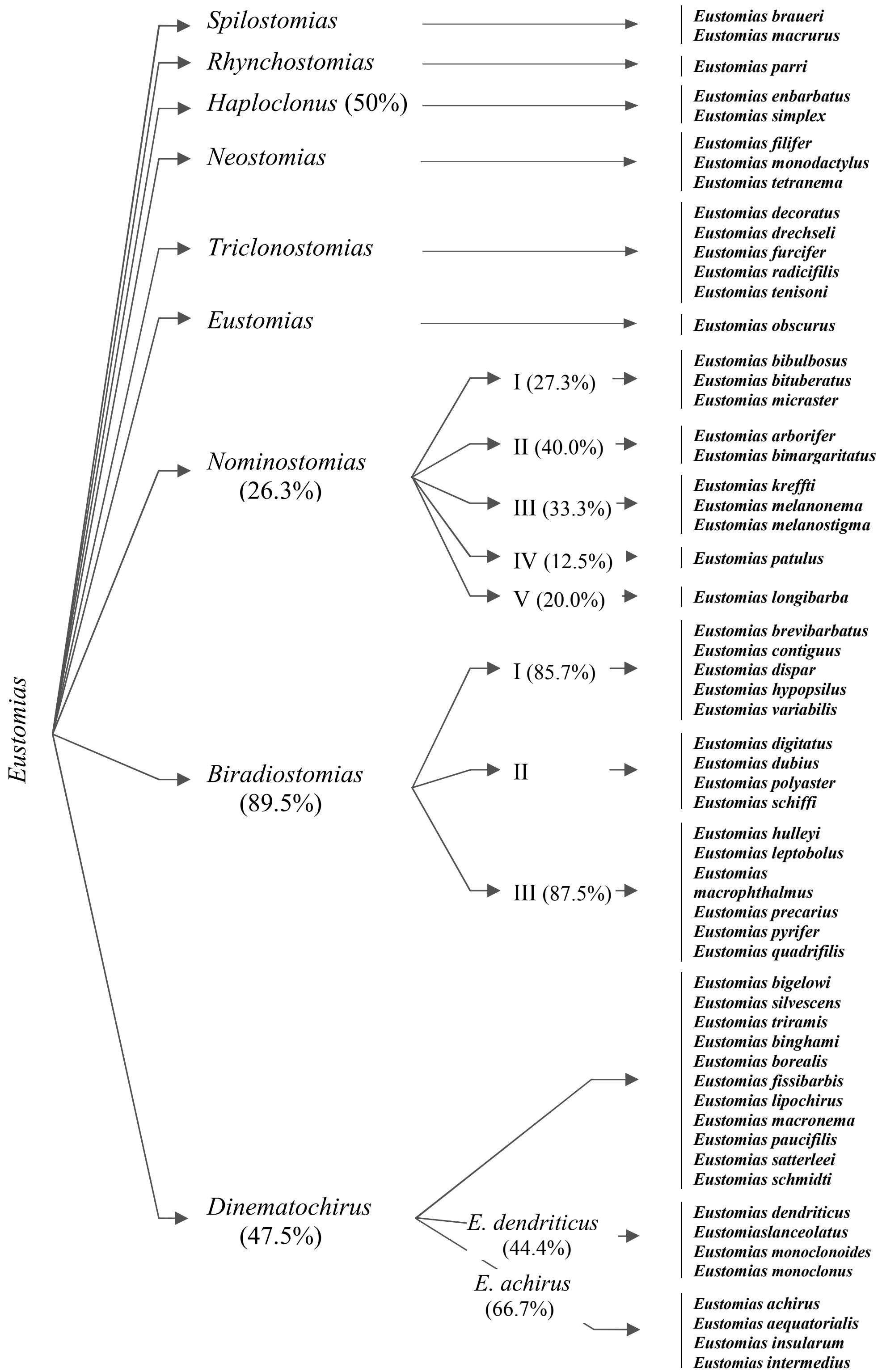


Figure 5.3 North Atlantic *Eustomias* species by sub-genus and species group (see text). Values associated with sub-genera and species group names indicate the percentage of North Atlantic species in relation to total number of species of the taxa; if no value is given then 100% of the species occurs in the basin.

astronesthids are the second most speciose sub-family, because of *Astronesthes*, followed by the Stomiinae, Malacosteinae, Chauliodontionae and Idiacanthinae.

The North Atlantic Stomiidae assemblage

The Stomiidae species assemblage reported for the North Atlantic comprises 141 species distributed over 24 genera. These correspond to more than 50% of the stomiid species currently recognised (Table 5.1). A checklist of those stomiids is given in Appendix E. The number of specimens and the biomass per species for the entire sample is given in the Table G.1 (Appendix G). The top 20 species in terms of abundance and biomass are also ranked in that table.

Only two (monotypic) genera have not been reported from the basin, *Odontostomias* is an eastern Atlantic endemic and the monospecific *Chirostomias* lives only in the subtropical belt of the North Atlantic. Excluding the genera that consist of one or two species, *Photonectes* and *Aristostomias* showed the highest proportion of species incidence in the North Atlantic (83.3%); the numbers of *Eustomias* species reach about a half (Fig.5.3) of the total, whereas *Astronesthes* and *Chauliodus* species are much more diverse elsewhere (25% and 37% respectively).

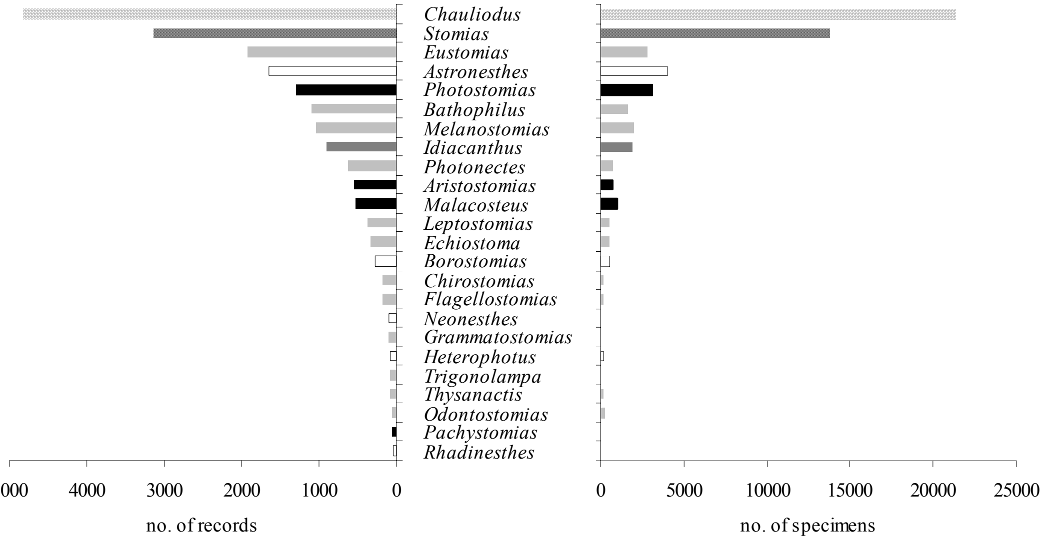


Figure 5.4 Total North Atlantic Stomiidae sample composition by genera (number of records n = 19497; number of specimens n = 56331). Bar patterns correspond to sub-families (see Fig. 5.2).

As a whole the genus *Chauliodus* accounted for the highest numbers of specimens and occurred more frequently, followed by *Stomias* (Fig. 5.4). *Eustomias* is the third ranking genus with more records in the database, reflecting its species richness (Fig. 5.3), but both *Astronesthes* and *Photostomias* contributed with more specimens. These last two genera were also among those that occurred most frequently. The top five ranking genera pertain to different sub-families. *Idiacanthus* was the eighth in terms of occurrences but ranked sixth in number of specimens, between *Melanostomias* and *Bathophilus*. A relatively smooth gradient throughout the remaining genera is apparent.

Chauliodus sloani not only produced more records and specimens but also produced the highest biomass (Table G.1). *Stomias boa* (both sub-species) was ranked the second in all these variables. *Chauliodus danae* ranked third in terms of occurrences and number of individuals, but its biomass was relatively low, reflecting its small size. Other important species in terms of occurrences and abundance were *Photostomias* cf. *guernei*, *Idiacanthus fasciola* and *Bathophilus vaillanti*. The melanostomiid that produced the highest biomass was *Echiostoma barbatum* that attained larger average size. Abundant species such as *Astronesthes niger* and *Eustomias obscurus* are either relatively small and/or slender and were ranked lower in terms of biomass. Conversely the large-bodies *Echiostoma barbatum*, *Malacosteus niger*, *Borostomias antarcticus* and *Melanostomias bartonbeani* were moderately abundant but ranked high in terms of biomass. In conclusion, the top 20 species include components of the five sub-families and were responsible for 62% of records, 79% of the specimens and 88% of the biomass.

Taxonomic ambiguities at species level

Borostomias abyssorum (Koehler, 1896) is only known from the holotype that was caught at the Gulf of Biscay. Gibbs (1964) considered the validity of *B. abyssorum* to be dubious. The holotype of *B. abyssorum* was originally deposited in the Université of Lion and later transferred to the MNHN (Paris). However, the database of the museum notes that the type was not found in 1998. So, the opportunity to evaluate the validity of this species must wait its rediscovery.

Parin and Borodulina (2000) tentatively synonymised *Astronesthes cyclophotus* with *A. neopogon*. *A. cyclophotus* was considered to be the juvenile form of *A. neopogon*. Indeed the *S_db* contains only nine small specimens (20-57mm SL) of *A. cyclophotus*.

However, the database also contains at least seven juveniles (25-73mm SL) of *A. neopogon* (total 34 individuals), which contradicts the statement of the authors that only about ten large specimens (>100mm) are known. *A. neopogon* has a distinct barbel that makes its identification reasonably assured. The validity of the two species is maintained until further studies resolve this question.

Recently Parin and Borodulina (2002) reviewed the systematics of *Astronesthes niger* and split it in to eight species (seven living in the North Atlantic). Most of those species have meristics features within a similar range of variation and are distinguished mainly using the structure and distribution of luminous tissue on the head and body. However, only fish larger than 80-110 mm SL achieve the full development of these characters. Hence more than 95% of the known specimens of "*A. niger*", which are smaller than 80mm SL (according to *S_db* data), cannot classified by the key constructed by Parin and Borodulina (2002). So, in this study the *A. niger* species group of Parin and Borodulina (2002) has been treated as a single taxon.

The specific compositions of several genera are not completely clear. *Leptostomias* and *Melanostomias* need to be reviewed. Following Morrow and Gibbs (1964), Gibbs and Barnett (1990) noted that *L. gracilis*, *L. macropogon*, *L. longibarba* and *L. bermudensis* may prove to be synonyms. These species show photophore counts within the same range of variation and have similar barbel configurations (as *L. analis* and *L. leptobolus*). A revision of this species complex is required, but until further developments the six nominal species were retained.

During the Stomiidae survey made on the collections that hold mesopelagic fishes several *Melanostomias* specimens were found on the shelves labelled by R.H Gibbs as new (undescribed) species (e.g. UF and ZMUC). At least some were caught in the North Atlantic and probably belong to the two species that in Gibbs and Barnett (1990) were referring to as *Melanostomias* sp.

The genus *Odontostomias* is endemic in the Atlantic region off Africa between 15º N and 18º S. Norman (1930) described both species presently recognised (*O. masticopogon* and *O. micropogon*). Parin and Golovan (1976) and Gibbs and Barnett (1990) noted that the only character differentiating the two species is the relative length of the barbel, which may be size-dependent. Gibbs and Barnett (1990) concluded that "the status of the two nominal species needs investigation". The two species have been included in the database and will be considered valid until new decisions are made about their status.

When reviewing the systematic of the malacosteids, Goodyear (1980) re-evaluated *Photostomias guernei* and concluded that it is a species complex containing several species. He designated four *Photostomias*, two *Aristostomias* and one *Malacosteus* new species. Goodyear's thesis was never published so all his new species are not valid. Goodyear (1990) reported *Aristostomias* n. sp. and *Photostomias* n. sp (see also Gibbs, 1984e). As mentioned above the systematics of the genus *Photostomias* are being investigated by C.P. Kenaley and K.E. Hartel and "*P. guernei"* is a complex of species that will be split in several new species (T. Sutton, Harbour Branch Oceanographic Institute, comm. pers., 2004).

Other North Atlantic nominal species were found to have an uncertain status. According to Clarke (1974) and Gibbs and Barnett (1990), *Photonectes achirus* Regan and Trewavas, 1930 may be a synonym of *P. caerulescens*,). The *S_db* contains nine specimens assigned to the species and a specimen of *P. achirus* was reported from the Gulf of Mexico (Sutton and Hopkins, 1996a). The species will be considered valid until further developments. *Eustomias globulifer* Regan and Trewavas, 1930 and *Eustomias micropterygius* Parr, 1927 were considered *Nomen dubium* by Gomon and Gibbs (1985), as they are only known from the holotypes, which are juveniles incompletely metamorphosed and probably with damaged barbels.

Conclusions

The status of the present knowledge about the systematics of Stomiidae seems adequate to support an "ecological" approach to its biogeography and biodiversity. However, the absence of truly phylogenetic studies at specific level for most of the taxa (i.e. except *Stomias* and *Aristostomias*), combined with the lack of palaeontological evidence about the evolution of the group, does compromise any attempt at analysing its evolutionary (historical) biogeography. Moreover, and according to Harold and Weitzman (1996), the generic interrelationships obtained by Fink (1985) though convincing, need further investigations.

The resolution of known systematics uncertainties for some genera may increase (or even decrease) the numbers of known species, which will bias the patterns of species distributions. The plot of new species descriptions with time (Fig. 5.5) shows a clear tendency for the number of species to increase as a result of the new systematics reviews. It is uncertain whether or not this tendency will continue in the future. However, it is most likely that a critical re-examination of *Leptostomias*, *Photonectes*, *Melanostomias*, *Photostomias* and *Aristostomias*, will result in the description of further species. Moreover the use of molecular techniques may reveal that cryptic species are much more common than thought, especially among the taxa that maintain disjunct distributions in various oceanic basins (e.g. Miya and Nishida, 1997, 2000).

Such systematics revisions of the group will require a re-evaluation of the conclusions of this study (Chapter 6 and 7). Although, any such changes are unlikely to result in any drastic revisions in the overall picture of the Stomiidae systematics, biogeography and biodiversity.

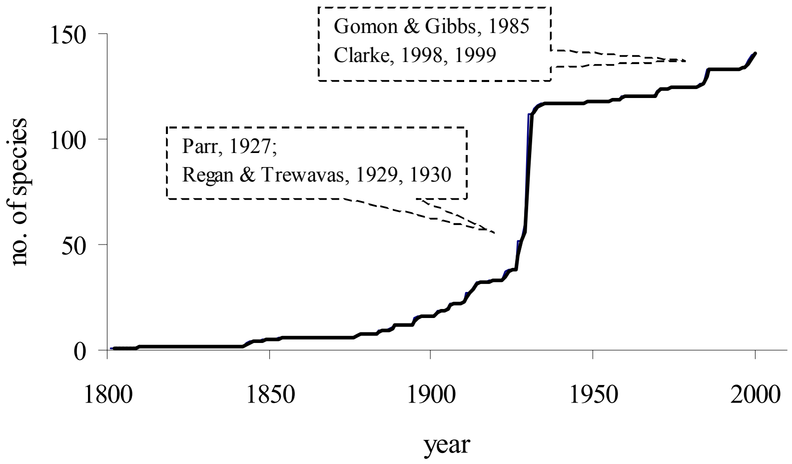


Figure 5.6 Cumulative number of North Atlantic Stomiidae species per year of description

Finally, the use of molecular approaches to Stomiidae, similar to those presented by Miya and Nishida (1996, 1998, 2000) for other Stomiiformes taxa may result in some major redesignations of the systematics.

Also there is a great amount of cleared and stained material are available in several museums, which can be used to support complementary morphological phylogenetic studies, especially at the species level (see Weitzman, 1967b; Goodyear, 1980; Fink, 1981, 1985, for a list of material available in this condition).

Chapter 6 - Biogeography of North Atlantic Stomiidae

Introduction

Most studies on pelagic biogeography have focused on planktonic invertebrates. This is reflected in the biogeographic atlas produced by van der Spoel and Heyman (1983): of the three hundred species then mapped, only twenty are micronekton fish (and eighteen mammals). However, the first pelagic biogeographic studies all dealt with midwater deep-sea fishes (e.g. Ege, 1934, 1948; Bruun, 1936). After those pioneering studies, the discipline evolved based on advances made in physical and biological oceanography (Sverdrup et al., 1942) and profited from material collected, essentially, by the “Dana” Expeditions. Haffner (1952) and Ebeling (1962) are representative studies of that period. Midwater pelagic biogeography became established as a scientific subject in its own right and at least two large-scale biogeographic programs were carried out to explore the Atlantic Ocean. These programs produced a huge amount of material, which underpins many publications (e.g. Backus et al., 1965, 1969, 1970; Jahn and Backus, 1976; Krefft, 1974, 1976; Hulley, 1981; Hulley and Krefft, 1985). Baird (1971) and Johnson (1982) published important studies on (global) biogeography of midwater fishes, but it was Backus et al. (1977) who improved our knowledge of Atlantic midwater zoogeography. Various other programs targeted the biogeography of midwater fish in the Pacific Ocean (e.g. Barnett, 1983, 1984; Willis, 1984; Clarke, 1987). The zonal distribution of faunal communities in that oceanic basin has proved to be far more even than in the Atlantic (especially the North Atlantic).

Theoretical aspects of pelagic biogeography were systematically reviewed (e.g. van der Spoel and Pierrot-Bults, 1979; van der Spoel and Heyman, 1983; Pierrot-Bults et al., 1986; Angel, 1994; Pierrot-Bults and van der Spoel, 1998) and an eclectic perspective emerged. However, a standardised methodology, useful for further developments of the science, has not been achieved (Pierrot-Bults, 1998; Longhurst, 2001).

Biogeographic sub-divisions of the ocean

The first consistent pelagic biogeographic analyses (e.g. Pickford, 1946) used temperature-salinity profiles, which characterised different water masses. Presence-absence of a species in a specific water mass led Ebeling (1962) to classify the faunas in broad distributional patterns. They were considered "attached" to those water masses and constrained by the effects of hydrographical features. Distribution was related to temperature, productivity, dissolved oxygen, etc. Ebeling (1962, 1967) created a hierarchical areal system that sub-divided the ocean into faunal (or zoogeographic) zones. Other authors (e.g. Baird, 1971) adopted similar procedures: as physical properties, the water masses appeared to be characterised by their biological properties as well. Following this trend, Backus et al. (1977) created their own areal partitioning of the Atlantic. The final result was obtained by combining individual species distribution patterns (of Myctophidae) with the observed faunal boundaries, which conformed to recognised hydrological features. Johnson (1982) criticized the methodology implemented by Backus et al. (1977) based on several inconsistencies. However, the system was used as the main framework for his biogeographic approach to the Atlantic (as it was for several others authors).

Many of the biogeographic sub-divisions of the ocean were based on distribution of pelagic species (or species assemblages), and despite their broad similarity, the inconsistencies are evident (see for example van der Spoel and Heyman, 1983 and Dinter, 2001). The variety of biogeographic maps demonstrates the weakness of methodologies and data used to produce them. Although different taxonomic groups are expected to show different global distributions, reflecting their natural history and ecology, it is accepted that a unique biogeography exists (e.g. Marshall, 1979).

Distribution patterns

The definition of rational patterns to fit species with recurrent distributions is a common practice when analysing the biogeography of pelagic organisms (e.g. Ebeling, 1962; Krefft, 1974, 1976; Backus, et al, 1977; Hulley, 1981; Johnson, 1982; Parin, 1984). Some of those schemes are hierarchical, others not; most use the classical boreal, subtropical, tropical and equatorial terminology; others are more linked with the general hydrology and term the patterns as central, peripheral, transitional, etc.; some incorporate the affinity of a species for a particular range of e.g. temperature; several treated the species solely as "pelagic"; others include the vertical distribution of species (meso- and bathypelagic) and/or their dependency of the neritic environments (pseudoceanic or distant-neritic); some are applied to global scale distributions; others are based on the occurrence at different oceanic basins. Most of those systems, however, were established on presence-absence data or, at the best, on relative abundance computed from a limited set of material, normally collected by one or several field programs.

Some authors found that a relatively small number of biogeographic patterns can accommodate all the existing distribution ranges. Backus et al., (1977) included 105 Atlantic myctophid species in 9 distribution patterns. At the other extreme van der Spoel and Heyman (1983) described 150 types of distributions, which is about one pattern for every two species. There does not appear to be a consensus, except when the faunas are classified into broad, large-scale patterns (i.e. warm water vs. cold water, etc.) or have clear disjunct distributions (e.g. bi-antitropical).

Mesoscale biogeographic studies

Often, the analyses of biogeographic processes at the mesoscale allow a better understanding of the processes at a global scale. Ebeling (1967) first postulated that biogeographic issues are better inferred by multivariate statistics (as a response to the multi-factors that affect the distribution of species). Subsequently, several authors used cluster analysis and other multivariate techniques to identify faunas and to detect their relationships and faunal changes at boundaries (e.g. Jahn and Backus, 1976; Hulley and Krefft, 1985; McKelvie, 1985a; Themelis, 1996). A review on regional factors that contribute to the clarification of the biogeography of North Atlantic midwater fauna is presented in Chapter 1.

Evolutionary biogeography

Only few studies have taken a consistent approach to historical (evolutionary) biogeography of mesopelagic fish fauna (e.g. White, 1994). As Johnson and Zahuranec (1998) stated, evolutionary biogeographic studies needs a solid phylogenetic background at the species level and need to extend the analysis at the global scale. These two premises cannot be fulfilled with the present knowledge, and constrains the development of new approaches. The recognition of "hydrotectonic events" in shaping the actual pelagic biogeographic patterns is largely accepted; however, the evolutionary mechanisms and pathways that drove to the actual biogeography are unknown.

The Ecological Geography of the Seas

Probably, the system of Longhurst (1995, 1998a,b) is the most important recent contribution towards an ecological and technologically driven pelagic biogeography. It is an analytical system that compartmentalises (in provinces and biomes) the environmental and biological (primary production) processes, which are expected to influence the distribution of pelagic fauna (at least epi- and mesopelagic faunas) (see Appendix A). However, the method does not include biotic interactions (e.g. competitive exclusion) that may generate modifications to the underlying patterns that are determined by productivity. Even so Longhurst's Ecological Geography of the Seas was adopted in this study as the framework to describe and analyse the biogeography of North Atlantic Stomiidae.

Biogeographic studies on Stomidae

Some stomiids are among the most common midwater fishes. *Stomias* and *Chauliodus* species were used in several biogeographic studies (Ege, 1934, 1948; Bruun, 1936, 1958; Haffner, 1952; Crane, 1966; Gibbs, 1969; Johnson and Zahuranec, 1998). However, the biogeography of the remaining stomiid genera and species has not been studied. The distributions of Atlantic members of the *Eustomias* sub-genus *Nominostomias* were used by Gibbs (1986e) to introduce to his species concept in a biogeographic context.

Obviously, the distributions of many stomiids were analysed in biogeographic studies that used the whole assemblage of micronektonic fish species. However, the majority of stomiid species are less abundant than other taxonomic groups (e.g. Myctophidae, some genera of Gonostomatidae and Sternoptychidae) and they have seldom been referred to in those pooled analyses.

Objectives of the chapter

1. To produce an Atlas of North Atlantic Stomiidae species; 2. to classify quantitatively the fauna in relation to its broad global distribution; 3. to describe and quantitatively to classify the observed distributions into subjective but coherent distribution patterns and sub-patterns; 4. to evaluate the relationships between the Longhurst's eco-biogeographic system and the observed patterns.

Material and Methods

Data source and basic computations

The data compiled in the Stomiidae database (*S_db*) are summarised in Chapter 2. The total net-hauls included in this study (n=8186) are plotted in Figure 2.3. Those used to compute the sampling effort summed 6839. They were classified by areal squares of 5º per 5º latitude/longitude (*sq_5x5*) and Longhurst's (1998b) provinces (*Lgh_P*) (Fig. 2.2).

The methods to compute the standardized fishing effort (*std_h*) carried out in those squares and provinces are presented in Chapter 4. The geographical distribution of the fishing effort per *sq_5x5* is given in Figure 4.3. The relative abundance of individual species per unit area was calculated by the ratio between the number of specimens and the standardized fishing effort (*n_spec/std_h * 100*).

A review of the systematics of the species involved is presented in Chapter 5. The distribution of individual stomiid species is presented in the Atlas of North Atlantic Stomiidae species (Appendix F). Data on global distribution of the species mapped are presented in Appendix E. A summary of the global distribution patterns observed is presented in Table 6.1.

Preliminary analyses suggested two additional provinces to the Longhurst eco-biogeographic system within the North Atlantic Tropical Gyral (NATR): the North Atlantic Tropical Gyral West (NATR W) and East (NATR E). The first is a narrow band limited by the southern boundary of the North Atlantic Subtropical West (NAST W) and the northern and west boundaries of the Caribbean (CARB) province. The NATR W coincides with the western tropical limb of the Subtropical-Tropical Gyre. NATR E extends longitudinally parallel to the Canary (CNRY) offshore to 30ºW and is interpreted as an extension of the Western Africa upwelling region. The north and south boundaries follow those of the NATR.

Distribution patterns of North Atlantic Stomiidae fauna

Biogeographic patterns and sub-patterns were created to accommodate the areal distributions depicted for the North Atlantic Stomiidae species (Appendix F).

As centres of abundance are often difficult to discriminate within collections sites, because of expatriation, the maps were analysed visually and the information combined with the data on specific relative abundance computed for each Longhurst provinces and biome (Table 6.2.).

The terminology used to define the patterns and sub-patterns roughly follows the Longhurst's system and is similar to that defined by Backus et al. (1977). The high diversity of geographical distributional ranges meant that most patterns were considered too heterogeneous and were split into many sub-patterns (Table 6.3).

In this study dispersal means the tendency of a species to be expatriated and to survive outside its main range. The main (or home) range of a species was identified as the area where the relative abundance of specimens is highest. The reproductive or the sterile ranges of the majority of those species are not known. The ability a species has to disperse was subjectively classified as the number of provinces where a species has been reported outside those considered its main range. The value was averaged for all the species included in a pattern or sub-pattern. This was also viewed as an indication of the extent of the distribution.

Distribution of Stomiidae and the Longhurst's system

The data matrix of stomiid species relative abundance per *sq_5x5* was used for the analysis. The *sq_5x5* were classified by the Longhurst's system (provinces and biomes). The multivariate statistical procedures (classification and ordination) followed the strategy described by Field et al. (1982), detailed by Clarke and Warwick (1994), and utilised in the ecological package Primer® 5 (Clarke and Gorley, 2001). The raw data were submitted to square root transformation and the Bray-Curtis similarity measure was used to compute the triangular similarity matrix. Then a multi-dimensional scaling (MDS) analysis was performed from the similarity matrix. The multivariate 1-way layout ANOSIM (R statistics) tested the null hypothesis of "there are no differences between the groups (factors)", which in the present case were the Longhurst's provinces. Then the raw data matrix was averaged according the Longhurst provinces (factors), and the same procedures were repeated. The matrix was used to produce a cluster analysis using group average sorting. To test if the data obtained for each of the provinces came from a linear sequences in space or seriation (i.e adjacent samples being the closest in species composition) the Primer 5 routine RELATE was applied to the similarity matrix.

Results

Broad distributional patterns of North Atlantic species

The North Atlantic has a high species richness of Stomiidae, compared to others oceanic basins (Chapter 5). In terms of the total stomiid species currently recognised, the level of North Atlantic endemicity is relatively low (16.7%), with about a third (31.9%) of the species present being endemic (Table 6.1). The majority of these endemics are *Eustomias* species (33), while other genera are represented by three (*Astronesthes*), two (*Bathophilus*) or one endemic species (*Chauliodus*, *Stomias*, *Chirostomias*, *Melanostomias*, *Grammatostomias*, *Leptostomias*, *Photonectes*). The monospecific genus *Chirostomias* is exclusive to the basin. A further nine species (seven *Eustomias* and two *Leptostomias*) extend southward from the equator within the equatorial Atlantic provinces (ETRA or WTRA). Additionally, ten *Eustomias* species, eight *Astronesthes*, two *Leptostomias* and *Odontostomias*, and one *Grammatostomias*, *Chauliodus*, *Stomias* and *Melanostomias* are Atlantic endemics. In total, 76 species representing 54.6% of the fauna reported to occur in the North Atlantic are Atlantic endemics.

Only two of the remaining 65 species, do not occur in the Pacific being found in the Atlantic and Indian oceans. Twelve are restricted to the Atlantic and Pacific and six of those species have never been caught in the South Atlantic.

The 36 species with disjunct North Atlantic populations fit into a number of patterns: 1) they can be endemic to the Atlantic (one *Astronesthes* and three *Eustomias*); 2) widely distributed in the three main oceanic basins (25 species from 12 genera); or 3) more rarely, occur in two oceans (seven species from five genera).

Distribution patterns of North Atlantic Stomiidae fauna

The following patterns were created to include the diversity of the geographical distributions depicted for the stomiid species in the North Atlantic (Appendix F) and the relative abundances of the species in the Longhurst's provinces (Table 6.2). Twenty-two patterns and 54 sub-patterns characterise the distribution of the fauna (Table 6.3). Eight patterns include species that shows relatively coherent or peculiar areal distributions and were defined without any sub-partitioning. They include one or several species. Others patterns are more complex, or heterogeneous, and have been subdivided into several sub-patterns to account for the diversity observed.

Equatorial

Sixteen species were classified under this pattern: two *Astronesthes*, *Heterophotus ophistoma*, *Thysanactis dentex*, four *Photonectes*, seven *Eustomias*; and one *Aristostomias*. The pattern was subdivided in 6 sub-patterns. The species that distribute exclusively in WTRA [i.e. *Equatorial (west)*] or in WTRA and secondary in NATR E and/or CARB accounted for ca. 81%. The remaining 3 species occur on both sides of the equatorial waters. The *Equatorial (west) - Caribbean (distant neritic)* includes three *Photonectes* and one *Eustomias* species that are confined to the continental and insular margins of the region. These Atlantic *Photonectes* are apparently isolated from the populations living elsewhere, and the *E. brevibarabtus* is a western Atlantic endemic species.

E. dispar is reported only from the equatorial waters of the North Atlantic, whereas *E. kreffti* and *E. intermedius* also occur in the southern Atlantic equatorial waters. More than 80% of these 16 species extend their ranges into the South Atlantic but from those only four are endemics from the Atlantic. Among the species that live in other oceanic basins, eight maintain Atlantic equatorial disjunct populations.

The equatorial species, on average, were reported in 4.9 Longhurst provinces (1 to 8). The Equatorial (west) species showed the lowest ability to disperse.

The distributions of *P. gracilis*, *E. intermedius* and *E. dispar* may prove to be different as in the North Atlantic these species are known only from few specimens (<5).

Equatorial complex

This pattern contains species that show their highest abundances at the equatorial waters but occurred in high numbers in several other provinces (e.g. in the subtropical belt). The six species include one *Melanostomias*, four *Eustomias* and *Pachystomias microdon*, which typified five sub-patterns.

E. dendriticus is endemic of the North Atlantic and *E. longibarba* distributes through the equatorial waters. The remaining species were reported in the Indian and Pacific oceans.

In general these species are able to survive in a number of Longhurst provinces (average 7.3). The distribution of *E. dendriticus* needs further evaluation because the species is known only from few specimens (<5).

Eastern Tropical - Equatorial

This pattern includes the species that evolved and occur along the western coast of Africa. Most of these species (i.e. 10% of the North Atlantic stomiid assemblage) are considered distant-neritic. This pattern contains 6 sub-patterns. The *Eastern Tropical - Equatorial (east); large range* is the most characteristic. It embraces four eastern Atlantic endemic species, which extend from the upwelling region off Mauritania to the upwelling zone associated with the Benguela Current. The other sub-patterns have more restricted distributions. The *Eastern Tropical; limited range* sub-pattern comprises two North Atlantic endemic *Eustomias* species (one living around Cape-Verde Islands) and the *Odontostomias masticopogon*. The *Equatorial (east) - Eastern Tropical* is a similar sub-pattern but the species show higher abundances at the Equatorial waters. *Eustomias melanonema* is endemic of the region. Finally the *Equatorial (east)* sub-pattern includes three *Eustomias* species that are known only from the Gulf of Guinea (ETRA).

These species normally are confined to the provinces where they reached the highest abundances. In average they spread through 2.9 provinces (1 to 5). However, *Astronesthes zharodi*, *E. insularum*, *E. patulus*, *E. lanceolatus* and *E. monoclonoides* are known only from few individuals and their distributions may prove to be different from those presented here. Two species have uncertain taxonomic status (*O. masticopogon* and *L. gracilis*; Chapter 6, Appendix F).

Eastern Tropical complex

This pattern includes two *Eustomias* species that occur in highest abundances at NATR E but distribute also throughout other regions such as the subtropical belt and Caribbean. The two species show different distributions and two sub-patterns were created to accommodate those differences. In average they were reported in 5.5 provinces.

E. monodactylus is a North Atlantic endemic species. The holotype of *E. achirus* is the only specimen known from outside the North Atlantic (Appendix F)!

Caribbean (distant neritic)

This homogeneous pattern includes 13 species (12 *Eustomias* and 1 *Photonectes*), which distribute mainly associated with the Caribbean arc. In average they were reported from two Longhurst provinces (1 to 4).

Ten of these species are endemic of the North Atlantic. *P. achirus* and *E. monoclonus*, both reported from other oceans, maintain isolated North Atlantic populations.

Eustomias digitatus, *E. leptobolus*, *E. precarious*, *E. pyrifer*, *E. silvescens* and *E. xenobolus* are known from less than five specimens.

Caribbean complex

This heterogeneous pattern includes eight species each of which show a peculiar distribution and therefore were subdivided in eight sub-patterns. All showed higher abundances at CARB but they occurred largely along the western North Atlantic. Their ranges extend on average through 6.3 Longhurst provinces (2 to 10), showing a high dispersal capacity.

These species belong to five genera (*Astronesthes*, *Echiostoma*, *Grammatostomias*, *Bathophilus* and *Eustomias*). Three *Eustomias* are endemic to North Atlantic basin and *A. similis* is not known outside the Atlantic Ocean. *Eustomias triramis* are represented only by four specimens.

Amphi-Atlantic (distant neritic)

This biogeographic pattern comprises 8 species from 7 genera (*Astronesthes*, *Borostomias*, *Stomias*, *Leptostomias*, *Melanostomias*, *Bathophilus* and *Aristostomias*) classed in three sub-patterns. The pattern is naturally heterogeneous as the species are linked differently with the distant-neritic environments where they are more abundant. Their ranges vary from that of *L. bilobatus*, which lives on slopes off Africa and Caribbean islands, to *Stomias affinis*, that spreads westward across the oceanic basin to 40ºW, at about 10ºN.

The sub-patterns defined reflect the latitudinal distribution of the species: some occur mainly in the tropical regions (i.e. NATR E and CARB) and were classified as *Amphi-Atlantic Tropical*; others (*Amphi-Atlantic Tropical – Equatorial*) extend to the equatorial distant neritic waters. These species disperse differently to the adjacent western or eastern provinces. Finally, there are species that dwell preferentially either on the eastern or western sides of the basin.

Only the two taxonomically related *Astronesthes micropogon* and *A. macropogon* are Atlantic endemics. All are reported from the South Atlantic and most occur elsewhere in the Indian and Pacific oceans.

The pattern includes species with moderate to high dispersal capacity; their geographic ranges spread out 5 to 11 provinces (average 7.6).

Northern Tropical - Equatorial

This pattern includes two wide distributed species that appear to maintain two relatively isolated meta-populations in the North Atlantic. The equatorial records of *M. tentaculatus* are disjunct from those of the South Atlantic. The equatorial population of *E. fissibarbis* spreads along the western South Atlantic to 27ºS, and is probably isolated from the Indian and Pacific populations. The species of this complex biogeographic pattern show different distributions and were classified under two sub-patterns. *Eustomias fissibarbis* and *Melanostomias tentaculatus* were reported in 7 and 9 North Atlantic Longhurst provinces, respectively.

Western Tropical Gyre

Four species were classified in this consistent pattern. These distribute mainly in the western tropical branch of the Subtropical-Tropical Gyre (NATR W). *Bathophilus schizochirus* is widely distributed in the three oceans, but it maintains a disjunct North Atlantic population. Two *Eustomias* species are endemics of the region and the remaining *Eustomias* also occurs in the South Atlantic. These four *Western Tropical Gyre* species disperse little outside the area considered.

Western Tropical Gyre complex

The twelve species included in this pattern attained their highest relative abundances at NATR W but also occurred in high numbers in other provinces (e.g. CARB, NAST W, NAST E, NADR or NATR E). These species were split in seven sub-patterns, which resulted from the combinations of the provinces where they are relatively abundant. The

Tropical Gyre – Caribbean and the *Tropical Gyre - Subtropical (west)* sub-patterns include half of these species. Often the *Western Tropical Gyre complex* species maintain isolated population units in the North Atlantic. On average these species occur across 5.8 provinces (2 to 9).

Five species (*A. neopogon*, *M. melanopogon*, *G. flagellibarba*, *E. bimargaritatus* and *E. macrophthalmus*) are North Atlantic endemics. *Eustomias simplex* extends its range into the South Atlantic. The six remaining species occur also in the Pacific Ocean (four in the Indian Ocean) but maintain North Atlantic populations.

Widely central

Two of the most common stomiids belong to this pattern: *Chauliodus danae*, a North Atlantic endemic species and *Idiacanthus fasciola*, that has an disjunct North Atlantic population. The widespread *Bathophilus longipinnis* is much less abundant and appeared scattered throughout the sub-tropical-tropical belt. *C. danae* and *I. fasciola* are abundant at the subtropical belt and along the North Equatorial Current, a region otherwise characterised by its dearth of stomiids. The region inhabited by *C. danae* is narrower than that of *I. fasciola* and *B. longipinnis*, both latitudinally and longitudinally. *C. danae* is absent from the inner Caribbean Sea and Gulf of Mexico.

Broadly Tropical

The *Stomias longibarbatus* is distributed throughout most of the North Atlantic warm water sphere. This species occurred in 11 North Atlantic provinces, but it is more abundant in tropical and equatorial provinces. The North Atlantic populations seems to be isolated from the others that live elsewhere.

Subtropical

This assemblage is relatively homogeneous and includes 13.5% of the North Atlantic stomiids (one *Astronesthes* and *Grammatostomias*, two *Photonectes*, three *Bathophilus*, and twelve *Eustomias*). The pattern was divided in four sub-patterns: species that occur across the NAST belt; the *Subtropical (west)* that comprises about 70% of these species; the *Subtropical (east)* that includes only two species; and the *Subtropical (west) - Tropical Gyre* that contains two stomiids that live in the North and South Sargasso Sea.

The subtropical species are North Atlantic endemics (63.2%) or otherwise sustain isolated North Atlantic populations. Only one of the non-endemic species (*B. altipinnis*) does not occur in the South Atlantic; the others can be classified as anti-tropical (or bi-subtropical). These species are more or less confined to the subtropical regions; in average they spread across 3.6 Longhurst provinces.

Eustomias decoratus and *E. drechseli* are known only from the holotype. Similarly *Bathophilus proximus* is represented by less than five individuals.

Subtropical complex

The species that fit in this heterogeneous pattern have their highest relative abundances in the subtropical belt but occur in significant numbers outside this region. The diversity of the species distributions was so high, that twelve sub-patterns were defined to include these sixteen species. Most of these (81.2%) are also distributed: 1) in the distant neritic environment of Eastern Tropical Atlantic, extending or not their ranges into the equatorial waters; 2) in the tropical zones of the western Atlantic (Tropical Gyre and/or Caribbean); or 3) in the boreal regions. These sub-patterns are stages of a series of complex distributions shaped by more or less isolated sub-population units often associated with the *Eastern Tropical – Equatorial Atlantic*. The *Subtropical complex* species are broadly distributed and, in average, they were sampled in 9.3 Longhurst provinces (7 to 14). The sub-pattern *Subtropical - Boreal (east) / Eastern Tropical – Equatorial* includes a peculiar widely distributed species (*Flagellostomias boureei*), which occurs throughout most of North Atlantic Provinces. It shows, however, a fragmentary pattern of distribution, peaking in the subtropical belt, in the North Atlantic Drift province and in Eastern Tropical Atlantic.

Taxonomically, these species belong to 11 genera, spread along the phylogenetic tree. The North Atlantic endemic *Chirostomias pliopterus* shows a subtropical-boreal distribution.

Only two of these 16 species are North Atlantic endemics and 5 are known only in the Atlantic Ocean. However, 8 species maintain disjunct North Atlantic populations.

Extended Eastern

This pattern accounts for *Rhadinestes decimus*, which has its core region in the temperate Northeastern Atlantic, but spreads from the eastern Arctic waters well into the Eastern Tropical Atlantic (*Polar - Eastern Tropical* sub-pattern). The species has been reported from the South Atlantic, Indian and Pacific oceans, but it maintains a disjunct North Atlantic population. *R. decimus* was reported in 6 Longhurst provinces.

Leptostomias haplocaulus is the other species classified under this pattern. It occurs chiefly between the eastern equatorial and subtropical regions, but some records have been made from the western tropical and subtropical waters. According to the present knowledge the species is considered also to live in the Indian and Pacific oceans.

Mediterranean – Extended Eastern

This monospecific pattern includes *Bathophilus nigerrimus* that lives in the Mediterranean Sea and spreads mainly along the Eastern Atlantic from the boreal to the equatorial waters. There are also scattered reports of this species for the western tropical and subtropical regions where it occurs at much lower relative abundances. *B. nigerrimus* occurs in Indian and Pacific oceans but it maintains a disjunct North Atlantic population (spreading into the equatorial waters as far as 9ºS).

Mediterranean –Eastern Tropical

The sub-species *Stomias boa boa* lives in the Mediterranean and along the adjacent Eastern Tropical Atlantic. This sub-species shows a little capacity to disperse outside its main range. It maintains an eastern Atlantic population separated from that living in the Southern Subtropical Convergence.

Boreal

The boreal pattern of distribution includes the eastern boreal *Trigonolampa miriceps* which is a bi-polar species occurring both in the North Atlantic and in the temperate regions of the Southern Ocean. Also preliminary classified as a (western) *Boreal* species is *Eustomias quadrifilis*, which is known only from the holotype caught at Slope Water. The distribution of this species may prove to be different as more specimens come available.

Boreal - Subtropical (east)

The highly abundant *Stomias boa ferox* typifies this pattern. This sub-species has a wide northern distribution that extends from the polar to the subtropical waters, showing higher abundances in the North Atlantic Drift province (NADR) and in the Slope Water (GFST). *S. boa ferox* lives only in the North Atlantic.

Polar – Boreal / Mediterranean (west)

Borostomias antarcticus is the sole stomiid that has a high latitudinal range in the North Atlantic. It occupies mainly the Polar seas, the eastern Boreal waters and the continental slopes at the northwestern Atlantic. *B. antarcticus* also maintains a relict population in the northwestern Mediterranean. As the species name indicates, this bipolar species also occurs circum-globally in the Southern Ocean around the Antarctica.

Widespread (anti-central)

Two of the most characteristic stomiids have this pattern: *Chauliodus sloani* and *Malacosteus niger*. Both avoid the central tropical waters, but are otherwise dispersed from polar to equatorial waters. *C. sloani* has highest abundances at GFST, but it is also very common in other provinces (e.g. MEDI, NWCS, NADR, NAST, CARB and WTRA). The species occurs in all the North Atlantic provinces and is ubiquitous almost everywhere in the World Ocean.

M. niger is more abundant at the equatorial waters but occurs in moderately high relative abundances in several other regions, including the polar seas. However, it has a narrower distribution range, compared to *C. sloani*, as it is absent from the Mediterranean and is relatively rare at the inner Caribbean Sea and Gulf of Mexico. *M. niger* is known from the Indian and Pacific oceans.

Uncertain patterns

Several taxa with systematics problems do not allow for a coherent description of their distribution patterns. These include the *Astronesthes niger*, several *Leptostomias* species, the genus *Photostomias* and *Aristostomias tittmanni*. See comments about those species in Chapter 5 (and Appendix F).

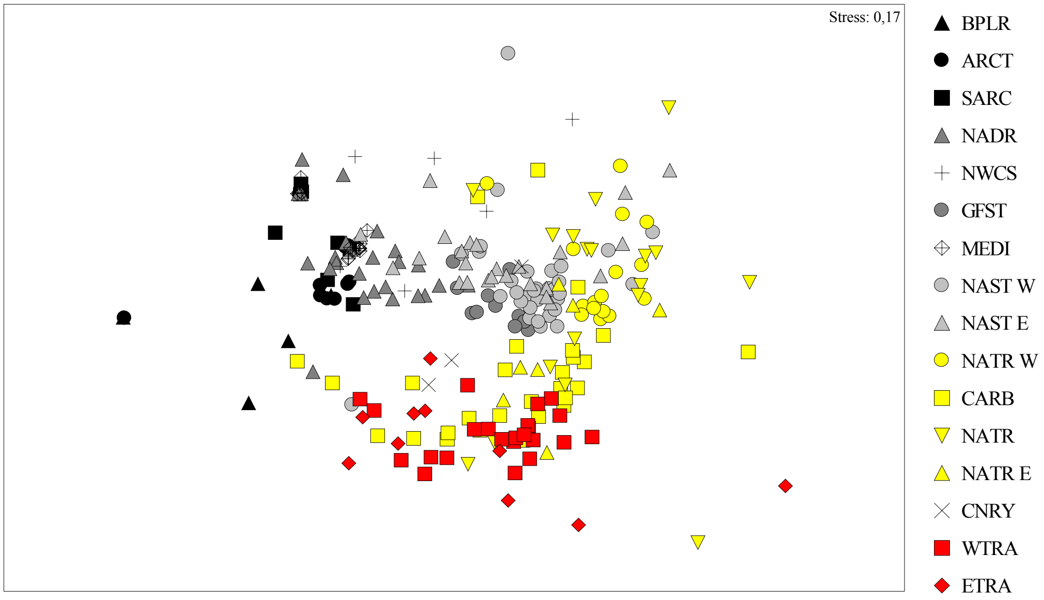


Figure 6.1. Multi-Dimensional Scale (MDS) plot for the relative density of Stomiidae species per *sq_5ºx5º* classified by Longhurst's (1998b) provinces (see Fig. 2.2 for acronyms full names). 1-way ANOSIM test: R=0.57; significance level 0.1%.

Stomiidae distribution and the Longhurst's eco-biogeographic system

The multi-dimensional scaling (MDS) plot for the 246 *sq_5x5* classified by Longhurst provinces is presented in Figure 6.1. The ordination shows an acceptable level of stress (0.17) to allow for a clear interpretation. Although a certain degree of ambiguity is apparent in the spatial classification of several squares, the dispersion also shows a tendency of many of *sq_5x5* to be grouped by provinces and biomes. The 1-way ANOSIM test accepts the alternative hypothesis that significant differences exist between samples from the 16 groups (provinces). Therefore to pool the data by Longhurst's provinces is a procedure supported by the 1-way ANOSIM test. The cluster dendogram and the MDS plot obtained from the matrix of relative abundance of species per Longhurst's provinces are presented in Figure 6.2. The general picture

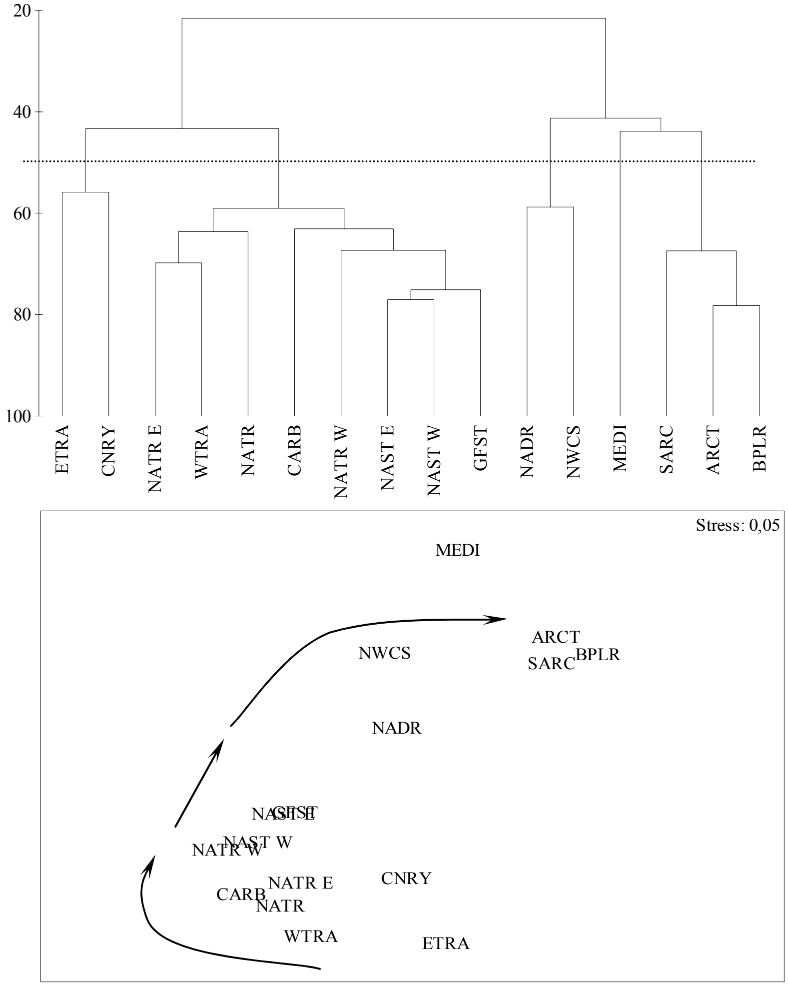


Figure 6.2. Cluster and Multi-Dimensional Scaling (MDS) analyses for data on relative abundance of Stomiidae species (*n_spec*/ *std_h*) per Longhurst's provinces (1998b) (see Fig. 2.2 for acronyms full names). (see the stress level in the plot). Arrows indicate the existence of seriation obtained from RELATE test: sample statistic ρ=0.737; significance level 0.1 %.

depicted by both analyses is clear. The eastern equatorial province (ETRA) is closely related to the western equatorial province (WTRA). The Canary/Mauritania upwelling region (CNRY) has a relatively anomalous position that, although its preferential association with ETRA, also has an apparent proximity to NATR E. Then the tropical NATR E, CARB and NATR grouped between WTRA and both tropical and subtropical Sargasso Sea provinces (i.e. NATR W and NAST W). NAST E follows in the sequence and it clustered preferentially with NAST W, but its proximity to GFST is apparent. To the north, and distinctly separated from the warm water sphere provinces, the NADR group with the NWCS. The impoverished MEDI holds an odd position between these latter provinces and the provinces that belong to the Polar Biome. Finally SARC, ARCT and BPLR are positioned together at the end of this northward progression. A general overview of the cluster analysis separates the provinces into three large groups: that formed by the ETRA and CNRY; that of the broad tropical-subtropical provinces, and that formed by the boreal/polar provinces. The RELATE test applied to the similarity matrix that generate both analysis shows the existence of a north-south spatial sequences (seriation in PRIMER terminology).

Discussion

The present study intends to improve the knowledge on the biogeography of stomiid fish in the North Atlantic. The data were distributed over a century in time and comprise a significant fraction of all the existing stomiid material collected in the North Atlantic, which in comparison to the others oceanic basins, has been thoroughly studied. According to the Stommel diagram (adapted to the space time structure of plankton patchiness by Haury et al., 1978 and to biogeography by Haury and McGowan, 1998) the data conform in terms of space-time scales. That implies that during a hundred years, this large-scale system has remained relatively stable; this is the biogeographic dimension. The present-day patterns of distribution have been shaped by the large scale circulation patterns, by the dynamic of the pelagic “populations” and by the ecological (physiological) tolerance of the species considered (e.g. Brunn, 1936; Parin, 1984; van der Spoel, 1986, 1994b).

Global distribution of Stomiidae

Without doubt, the North Atlantic is the best-studied basin in all senses. The uneven scientific coverage of the oceans (see e.g. Boltovskoy, 1998) is probably more marked when the midwater environment is considered. Consequently, many rare stomiids, or seldom caught by conventional samplers, may remain undetected in a particular region because of inadequately sampling effort. In this context, inferences about a global biogeography of Stomiidae are limited by the inadequate coverage of many oceanic regions.

The statement that several groups of Stomiidae radiated preferentially in the North Atlantic should be treated with reservation. However, the basin shows higher species diversity of stomiids when compared with other regions that have also been extensively surveyed (e.g. northeastern Pacific and Tropical Eastern Pacific). The compilation of global distributional data on North Atlantic stomiids has not been exhaustive, and therefore supplementary information will certainly change the broad picture detailed in this study. Anyway, it is apparent that many widely distributed "taxonomic" species (as we presently recognise them) have disjunct distributions in several oceanic regions. The level of genetic divergence across the range of those species is unknown, but it is expected that reproductively isolated groups will evolve in different directions (the ultimate process of allopatric speciation) (Marshall, 1963; Pierrot-Bults, 1997; Miya and Nishida, 1997). Moreover, species without any conspicuous phenotypic divergence may in fact be genetically diverse, as Miya and Nishida (2000) found for *Gonostoma ebelingi*. In the end, the species richness of North Atlantic Stomiidae is probably much higher than that that can be assumed by an evaluation based on presence-absence of Linnaean species.

The Stomiidae distribution patterns

It is apparent that geographical distributions are species-specific, as all the biological properties. They reflect the evolutionary history of the species in relation to that of the biotic and abiotic environment. A system to classify and categorize species into hermetic biogeographic patterns is obviously artificial and subjective. The proliferation of these schemes illustrates well that subjectivity (e.g. Ebeling, 1962, 1967; Baird, 1971; Krefft, 1974, 1976; Backus et al., 1977; Hulley, 1981; Johnson, 1982). The number of patterns, and the detail of the systems they integrate, depends of the organisms under study, the scales (spatial and temporal) of the analysis, and of the accuracy and definition of the data available. Moreover, the systematics gaps or the incapacity to identify "biological" species on most groups also constrain the accuracy of actual distribution ranges. Similar ranges create what is called generalised distribution patterns (or tracks), and the recognition of those patterns is traditionally a basic requirement of biogeographic analysis. However, patterns of distribution of the stomiid in the North Atlantic are very diverse, and to reduce them to a finite number of standard patterns, even numerous, was a difficult task. The process was assisted by the combination of visual and quantitative data, but a certain dose of subjectivity and uncertainty is still evident. Moreover, many species are known only from few specimens and their distributions may change as more individuals can be included in the analysis.

Some species have ranges that can be unambiguously classified (e.g. *Eastern Tropical Atlantic*; *Caribbean*, *Subtropical*). However, between each obvious pattern and another, there are several intermediate or even "exotic" patterns. Eight specific patterns and 14 heterogeneous patterns, comprising 63 sub-patterns, were created to accommodate the distributions of 141 stomiid species. The ratio of the number of species per pattern or sub-pattern is much lower than that found by Krefft (1974, 1976), Backus et al., (1977), Hulley (1981) and Johnson (1982), among others. However, that diversity of distributions agrees with the data presented by Heyman and van der Spoel (1983) that fitted one or two species in most of the global patterns illustrated.

Stomiidae distribution and the Longhurst's system

Although the stomiid distribution data supported relatively well the recognition of the biogeographic compartments of Longhurst (see below), most probably the simply spatial analysis of the data would not delineate the provinces as they were defined by the author. Most of the classical biogeographic systems combine the observed faunal distributions with the recognised hydrological large scale features (e.g. Ebeling, 1967; Backus, et al., 1977; Beklemishev et al., 1977; Johnson, 1982; and other in Van der Spoel and Heyman, 1983). Moreover, as noted by Johnson (1982) most of those biogeographic systems gave the primacy to physical oceanography to depict the provinces' boundaries. Often those systems lose the ability to recognise faunas because usually the species distributions extend far beyond the pattern to which they were assigned. Probably most of the generalised tracks defined were oversimplifications. A general conclusion is that data on pelagic fauna distribution *per si* seem to be inpractical for the definition of a consistent biogeographic system. In this sense, instead to create another areal subdivision of the North Atlantic based on the distribution of stomiids, which would be necessary simplistic, the recognised Longhurst (1998b) system was adopted to study and describe the complex distribution patterns of those midwater fishes.

Only a few stomiid species, mostly known from a few specimens, occur exclusively in one of the eco-biogeographic provinces. The majority of the species spread across the "leaky" hydrological boundaries and so live in a range of provinces or even biomes.

However, if relative abundances are taken in consideration, it is clear that many populations have the core (or cores) of their distributions in specific regions, and so records from elsewhere were expatriates. The observations correspond to the “Member-Vagrant” hypothesis presented by Longhurst (2001).

Based on the spatial distribution of species abundances, it was shown that most provinces have specific faunas (Figs. 6.1 and 6.2; Chapter 7). However, some provinces were found to be less homogeneous than others, which may indicate that those compartments include sub-regions with different environmental and ecological conditions. The most conspicuous heterogeneous province in the Longhurst system was the North Atlantic Tropical Gyral (NATR). It accommodates clearly three distinct stomiid assemblages: one at the northwestern NATR (coded herein as NATR W), associated with the tropical flank of the “eye” of the anticyclonic gyre (i.e. roughly the Southern Sargasso Sea of Backus et al., 1970, 1977); a second at the eastern NATR to ca. 30ºW (coded NATR E), as an oceanic extension of the coastal upwelling system (CNRY); and the central NATR, which is a vast oligotrophic region with low diversity and abundance of many stomiid species. The Eastern Tropical Atlantic (NATR E/CNRY) was first recognised by Backus et al. (1977) as a distinct biogeographic province: the *Mauritanian Upwelling*. John and Zelck (1998) based on ichthyoplankton distribution and on the dominant currents, redefined the concept of the *Mauritanian Upwelling* province of Backus et al., (1977) (see below).

The Caribbean Province (CARB) proved also to be relatively heterogeneous, with many species (e.g. subtropical) occurring only at the Gulf of Mexico but not in the southern Caribbean Sea or in the Lesser Antilleans, and vice-versa. In fact, Longhurst (1998b) recognised that two distinct ecosystems were classified under CARB. The author stated that the southern basin of CARB and the Gulf of Mexico “are rather dissimilar in their production processes…” and consequently it would be reasonable to consider them as ”…two different provinces”. But the author combined both provinces as for convenience.

Finally the eastern North Atlantic Subtropical Province (NAST E) appears to be cut-off latitudinally by the Azores Current (see below). Many species that occur at the southern part of this province clearly do not extend their ranges to the north of the current.

Mosaic species

Numerous stomiid species (as many other pelagic organisms) have disjunct populations in different oceanic environments and basins. In this study it was observed that various stomiids maintain several demographic units within the North Atlantic basin that are either geographically isolated from each other (e.g. *Neonesthes capensis*, *Flagellostomias boureei*; *Melanostomias biseriatus; Bathophilus brevis; Pachystomias microdon*, and all the amphi-Atlantic distant neritic species) or connected by narrow corridors generally along boundary currents (e.g. *Astronesthes gemmifer*; *Melanostomias bartonbeani*). Most of the species that show those units occur recurrently at the Eastern Tropical Atlantic and elsewhere, and were classified under complex biogeographic patterns. The existence of boreal midwater species living in the distant-neritic niche of the Eastern Tropical Atlantic (and Mediterranean) is not new (Backus et al., 1977, Badcock, 1981, John and Zelck, 1998). However, many species also have disjunct distributions in other regions (e.g. those classified *Equatorial (west) / Caribbean / Subtropical* or *Northern Tropical - Caribbean / Equatorial*). The distributions maintained by those “mosaic species” probably should be interpreted as an expression of the hierarchical nature of the distributional variability (patchiness), that ranges over scales of meters (hours) to thousands of kilometres (centuries) (see Haury et al., 1978; Haury, 1986; Haury and McGowan, 1998). The phenomena may be an artefact reflecting, for example, an uneven sampling coverage or inaccurate identifications, but its recurrence in the distributions of many species indicates that it is probably a real biogeographic pattern. It should be noted that Haury and McGowan (1998) did not mention this scale of variability (“meta-populations”), bounding from patches, limited by edges, to populations, limited by margins.

Those intra-oceanic demographic units stand at an intermediate scale between inter-oceanic disjunct populations and patches induced by mesoscale eddies for example. The ecological concepts of meta-populations are better developed in a terrestrial (insular) context (Whittaker, 1998; Cox and Moore, 2000). The recognition of those structures in the pelagial seems to be neglected (see van der Spoel, 1994b) or only superficially discussed (Angel, 1997). If self-sustained meta-populations, actually exist in the (midwater) pelagial they would represent an ecological advantage, in relation to restricted distributed populations, ensuring the resilience of a species facing dramatic or extreme events (ENSO or NAO like, or others non-cyclical) that lead to collapse of one or more of those demographic units. If dispersal is occurs, colonization from nearby meta-populations will establish the equilibrium of the system. These complex patterns of distribution would be an intermediate stage between to live only under a limited range of ecological conditions and to live everywhere (i.e. to be ubiquitous) and cope successfully with a vast range of biotic and abiotic conditions. The last stage of distribution was achieved only by *Chauliodus sloani* and to some extent by *Malacosteus niger*; *Flagellostomias boureei* perhaps will be ubiquitous in the forthcoming evolutionary step.

As mentioned before several "mosaic-species" maintain demographic units connected by narrow corridors along boundary currents, while the units of other species are apparently isolated. The level of reproductive isolation amongst those meta-populations is unknown. Polytypy is widely documented in many midwater fish species (Johnson and Barnett, 1972, 1975; Badcock, 1981; Johnson, 1986; Badcock and Araújo, 1988; Gartner, 1998; among many others) although it is not weather or not this variability represents ecophenotypic expressions or true genotypes. Nevertheless, if the isolation of those demographic units is maintained for large enough periods to allow genetic divergence, then formation of meta-populations will favour speciation. Moreover, the interruption of the existing pathways during geological cycles could hypothetically produced alternate periods of connection and disconnections of those units. The subject of meta-populations in the pelagial deserves further insights.

General circulation and the distribution of Stomiidae

A composite map of the general circulation of the upper layers of the North Atlantic is presented in figure 6.3.

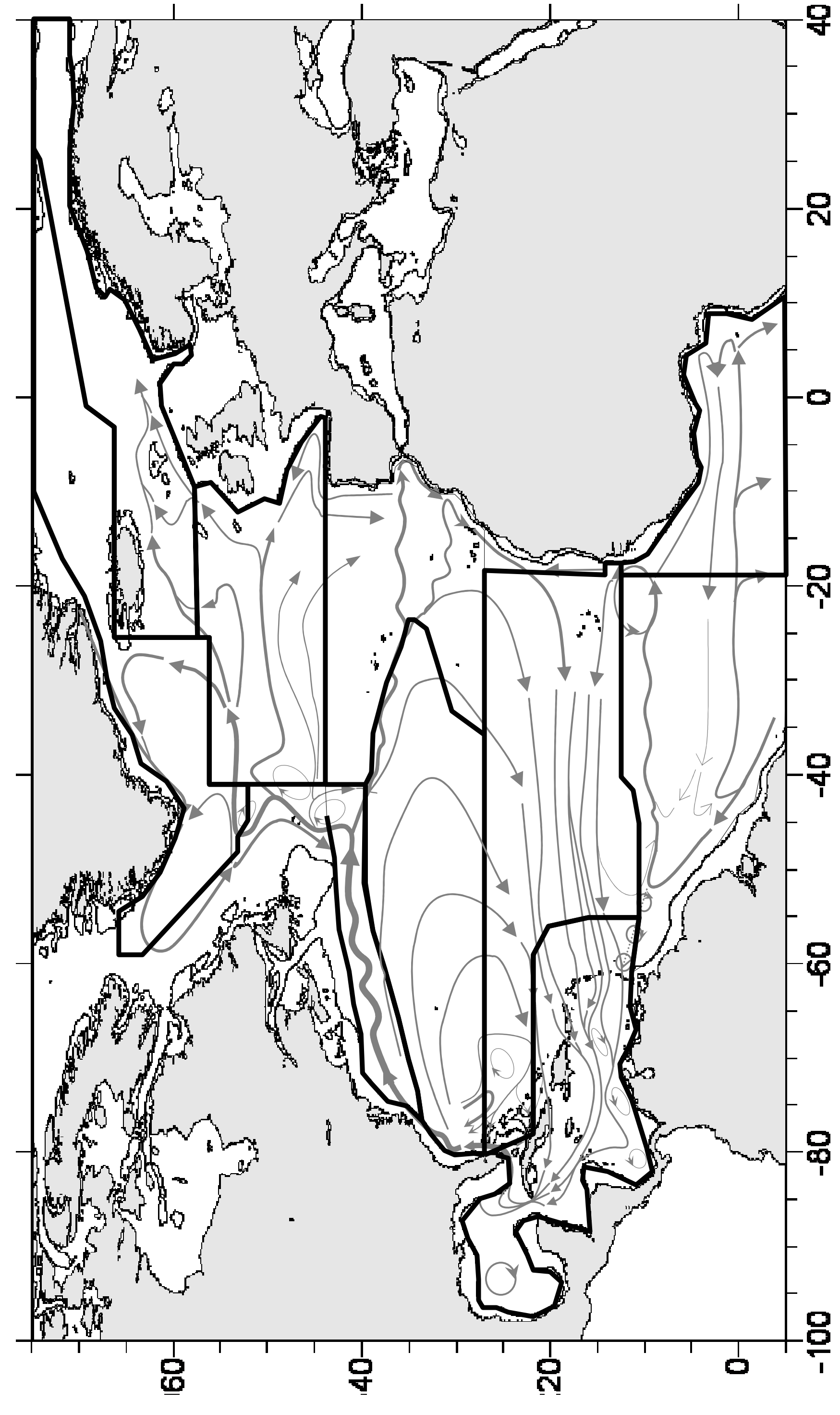


Figure 6.3. Sketch of North Atlantic upper layers general circulation. Data compiled from: Alves and Verdière, 1999; Bearman,, 1998; Bourlès et al., 1999; Dengg, et al., 1996; Hernández-Guerra, et al., 2001; Johnson and Stevens, 2000; Käse and Krauss, 1996; Krauss, 1996b; Lavender et al, 2000; Longhurst, 1998b; OSPAR Commission, 2000a,b; Schott and Molinari, 1996; Stammer and Böning, 1996; Stramma, and Schott, 1996; Stramma et al. 2003; Siedler and Onken, 1996.

Since Sverdrup, et al. (1942) physical oceanography has been definitively incorporated in the pelagic biogeography. The role of water masses and general circulation on the distribution of pelagic species is recognized. One question that often is formulated is how mesopelagic and bathypelagic species respond to upper oceanic currents (most extending downward to ca. 1000m) that shape the ranges of epipelagic species. This work indicates that stomiid fish distributions are constrained by the general oceanography of the upper layers and probably respond to the ecological processes that takes place in the photic zone (as observed by Fock et al., 2004). Note that most of the catches (ca. 83 %) were made in the epi- and mesopelagic layers (i.e. to 1000 m depth; Chapter 3) and that the somewhat loosely biogeographic boundaries of Longhurst's provinces (which accommodate acceptably the distribution of stomiids) broadly coincide with the major physical hydrological features. The effect of deep-water currents on the distribution of the bathy- and abyssopelagic species, is still difficult to access in detail, even if those currents are now far better known than some years ago. The knowledge about those communities are still very scarce.

The equatorial system of currents

The interruption of species distributions at the equator, and the low sampling effort undertaken in the southern latitudes of the equatorial waters, limit the definitive interpretation of equatorial patterns of distribution. The region is characterised by a complex system of zonal currents that are responsible for inter-hemispheric water exchanges that are not yet completely understood (e.g. Longhurst, 1998b, Stramma et al., 2003). As the multi-branched South Equatorial Current (SEC) feeds all the system, it would be expected to carry northward those species that have their core distributions in the southern hemisphere. However, this expectation is not supported by the data and, therefore, most of the equatorial species seems to have their centres of distribution at the northern sectors of the equatorial region. Possibly, the strict *Equatorial* species maintain their populations by having their life history strategies coupled with the system of currents and countercurrents that cross the region.

It is accepted today that the North Brazil Current and Undercurrent (NBC/ NBUC system), which cross the equator parallel to the northeastern coast of South America, do not enter directly into the Caribbean Sea at least between July and February (Johns et al., 1990, 1998; Bourles et al., 1999; Fonseca et al., 2004). Instead, the currents retroflect eastward at about 6ºN and feed the North Equatorial Countercurrent (NECC) and the North Equatorial Underwater Current (NEUC) that run eastward across the basin at about 5 to 10ºN. The anticyclone retroflection of the NBC generate large meanders that develop into giant eddies, which spin northwestward to the Lesser Antilles and disintegrate (Fratantoni et al., 1995). Some equatorial species (e.g. *Heterophotus ophistoma*, *Thysanactis dentex*, among others) have their centres of distribution at WTRA, and the specimens reported from the southeastern Caribbean probably are transported passively from the main stock by those eddies. The system also should act over the *Equatorial (west) - Caribbean (distant neritic)* species, and on the dispersal/ expatriation of species that have their centres of distribution in WTRA, that once having reached southern CARB may be transported northward to NAST W and GFST.

The NECC/ NEUC system is the oceanographic structure that lies at the boundary between the Western Tropical Atlantic Province (WTRA) and the North Atlantic Tropical Gyral Province (NATR) (Longhurst, 1998b). The northern limit of distribution of several equatorial species (e.g. *Thysanactis dentex*, *Eustomias brevibarbatus* and *E. kreffti*) is clearly bounded by those currents (some entering, however, the eastern and western tropical Atlantic). The NECC/ NEUC system is too the southern boundary of various species (e.g. *Idiacanthus fasciola*). The tropical form of the nycto-neustonic *Astronesthes niger* is distributed along a zonal band across the northern flank of the NECC, probably profiting from the upwelling associated with the thermocline ridge that lies between the NECC and the NEC.

The Gulf Stream

The thermohaline circulation at the western boundary of the tropical-subtropical Atlantic is the main hydrological feature of the basin. A substantial number of species classified as *Caribbean complex* have centres of distribution at CARB and disperse extensively into the adjacent subtropical province (NAST W) and/ or to the Slope Water (GFST). The effect of the Gulf Stream on the transport of specimens northward is quite a striking feature. Apart from species that leave the Caribbean and enter the anticyclonic gyral system, several others are relatively abundant in CARB, but relatively rare at the adjacent waters and moderately abundant in the Slope Water region (GFST). The distributions of *Astronesthes similis*, *Stomias affinis*, *Melanostomias melanopogon* and *Bathopilus digitatus* clearly follows a narrow path that lies along the western slope of North America connecting CARB and GFST. However, the fauna caught in the Slope

Water includes many other elements from subtropical, widely tropical, central, boreal faunas, etc. The GFST stomiids in general are larger compared to those from the adjacent warmer seas, but only *Stomias boa ferox* and *Chauliodus sloani* (among the stomiids) were found to be self-sustaining in the area (Themelis, 1996). Themelis (1996) reported that GFST community was structured on stochastic processes of mixing and advection of water and fauna, mainly from the Northern Sargasso Sea (NAST W). The present study confirms the observations made by the author (and by Jahn and Backus, 1976), that there are abrupt variations in the relative abundance of many stomiids between the Slope Water and Sargasso Sea (see Table 6.2). Craddock et al. (1987, 1992) studied the effects of the warm-core-rings (WCR) on the dispersal of subtropical fauna into the slope water. These rings are probably the most direct source of warm-water fauna being advected into the region, but, as referred above, the transport of tropical fauna (from CARB) into the core of the jet of the Gulf Stream should not be neglected. GFST also contains elements from the cold polar waters (*B. antarcticus*) and from the eastern boreal region (*Trigonolampa miriceps*) probably transported by the Labrador Current and by the Deep Western Boundary Current. The differences found between the studies of Themelis (1996) and McKelvie (1985a) are a reflection of the regions sampled by both, as most of the stomiid species that are expatriated in GFST are only able to tolerate the ecological conditions of the warmer western Slope Water.

The northern form of *Astronesthes niger* that occurs preferentially at GFST disperses into the northern Sargasso Sea probably trapped in the cold core rings (CCR) that pinched off the Gulf Stream. Although *Stomias boa ferox* was considered a *Boreal* species, it was also frequently caught at the NAST W. The role of the cold core rings (CCR) and eddies on the dispersal (or expatriation) of those species into the Northern Sargasso Sea needs to be evaluated.

The North Atlantic Current

Many stomiids are unable to survive in the northern boreal waters but a few spread successfully through the Northwest Atlantic Shelves Province (NWCS), transported initially by the Gulf Stream extension and then by the North Atlantic Current and the northern branch of the Azores Current. One example is the northern form of *Aristostomias tittmani* that concentrates mainly at NAST W and GFST but enters

NADR and the northern NAST E, both regions dominated by the North Atlantic Current zonal jets (Käse and Krauss, 1996).

Further to the north the Polar Front associated to the northern limb of the North Atlantic Current seems to be the northern boundary for the subtropical species that are able to spread into in NADR. However, several boreal species were caught at low abundances in ARCT and BPLR (Magnússon, 1996; Sigurðsson et al., 2002) indicating their ability to cross that major feature.

The Azores Current

The Azores Current (AC) arises at the bifurcation of the Gulf Stream extension (i.e. at about 42ºN 48ºW) (Käse and Krause, 1996). It flows southeastward and crosses the Mid-Atlantic-Ridge at about 35ºN, just south of the Azores Islands (Alves and Verdière, 1999). Southwest of the Azores this meandering jet suffers its first division: one limb enters the core of the subtropical gyre while most of the water continues along its eastward path. Passing south of the Azores, the AC splits again into a northern branch, which meanders zonally to reach the Gulf of Cadiz, and a southern branch that flows first to the south and then to east to enter the Canary Basin, at about 30ºN (Johnson and Stevens, 2000). The current (that can be detected to 1000-1500m but shows a low surface signal) constitutes a boundary of the subtropical gyre and the northwestern boundary of the northern Sargasso Sea Water marked by the 18ºC thermostad (NAST W). The AC provides the major source of water to the eastern recirculation by feeding the Canaries Current (CC) (Johnson and Stevens, 2000). The western limb of the current is a boundary for several Subtropical western Atlantic stomiid species. Its eastern branch functions as an efficient boundary for several subtropical and tropical species that occur at the southern NAST E but not in the northern section of that province (e.g. *Neonesthes capensis*, *Astronesthes cyclophotus*, *Photonectes dinema*, *P. leucospilus*, *P. parvimanus*, *Melanostomias melanops*, *M. tentaculatus*; *Eustomias simplex; E. filifer*, *E. tetranema*, *E. longibarba*, *E. schmidti*, *Aristostomias lunifer*). However, strays of various tropical and western Atlantic species are reported from the Azores waters (and also from NADR). The intense anticyclonic eddy field that pinches off northward from the main axis of the current (Alves and Verdière, 1999) probably is responsible for the expatriation of those species. Domanski (1986) and Angel (1989) studied the effects of the Azores Current on mesopelagic invertebrates. The authors found variations in terms of biomass and vertical structure of the populations at both sides of the Azores frontal zone (i.e. western and eastern Atlantic subtropical waters), but no differences in terms of species diversity, as reported here.

The Canary Current and the Cape Verde Frontal Zone

The Canary Current (CC) affects the distribution of many stomiids. This boundary current is an important feature in the biogeography of the Atlantic. Several subtropical species (or with subtropical meta-populations) extend their ranges southward along the CC to about 20ºN (*Rhadinesthes decimus*; *Chirostomias pliopterus*; *Leptostomias gladiator*; *Photonectes braueri*; *P. parvimanus*; *Bathophilus vaillanti*; *Eustomias macronema*). Moreover, the region supports disjunct demographic units of several other species (e.g. *Bathophilus digitatus*; *Eustomias achirus*; *E. schmidti*) and is a pathway for meta-populations of species further to the south, often at the Cape Verde Frontal Zone (e.g. *Astronesthes gemmifer*; *Photonectes margarita*; *Melanostomias bartonbeani*). Outside the Mediterranean Sea *Stomias boa boa* extends southward along the CC.

Faunistically the region of the Canaries Current should be viewed as the northern extension of the Eastern Tropical Atlantic, despite the non-inclusion of that area in the Mauritanian Upwelling Province of John and Zelck (1998) (see below). The CC follows the slope along the Northwestern Africa to about 20ºN and then deflects to feed the sluggish broad westward flow known as the North Equatorial Current (NEC), which is detected to a depth of about 1000m (Siedler and Onken, 1996; Hernández-Guerra et al., 2001).

The Cape Verde Frontal Zone is a complex region where the high saline low temperature North Atlantic Central Water and the low saline high temperature South Atlantic Central Water meet (Klein, 1992). The frontal zone is the core of the Mauritanian Province of John and Zelck (1998). This province was considered by the authors to be myctophid dominated and devoid of endemics species (see also Hulley, 1981). In relation to the stomiid fauna this zone supports a mixture of faunas of different origins: distant-neritic meta-populations of several species that otherwise distribute elsewhere (e.g. *Photonectes leucospilus*; *Melanostomias melanopogon*; *Bathophilus brevis*; *Eustomias macrurus*; *E. monodactylus*; *Pachystomias microdon*); many equatorial species that spread northward through the Cape Verde Frontal Zone (e.g. *Astronesthes atlanticus*; *A. richardsoni*); broad distributed species (e.g. *Chauliodus* *danae*); and Eastern Atlantic endemic species (i.e. *Astronesthes caulophorus; Stomias lampropeltis; Chauliodus schmidti; Leptostomias gracilis*; *Odontostomias masticopogon; O. micropogon; Eustomias patulus*; *E. melanonema;* and *E. insularum*), which contradicts the previous statements about endemicity.

The extension of the distribution of several equatorial species into the NATR E (*Equatorial - Eastern tropical* sub-patterns) is probably because of the northward flow of the NECC/ NEUC system toward the Cape Verde Bight, where the Guinea Dome (centred at ca. 10ºN 22ºW) forms (Siedler et al., 1992; Longhurst, 1998b). Also the meta-populations of several "mosaic species" seem to be associated with that permanent cyclonic feature. Some of those equatorial species that spread through the Eastern Tropical Atlantic as far north as the Canaries Islands are probably transported by the undercurrent that flows northward below the Canaries Current (Hernández-Guerra et al., 2001).

Backus et al., (1977) and John and Zelck (1998) established the southern boundary of the Mauritanian Province at about 10ºN, which coincides with the meridional boundary of NATR E and of the distributions of many stomiids. However, some tropical species extend their range further to the south, well inside the eastern WTRA (e.g. *Leptostomias haplocaulus*; *L. gracilis*; *P. microdon* and most of the *Eastern Tropical – Equatorial* species). If the *Eastern Tropical* species especially those endemics that have large distributional ranges are thought to be evolved at the upwelling region, the extensions of their distributions across ETRA and southward, possibly is an expression of a dispersal phenomenon. Upwelling regions are points (or nodes) of stress where speciation is expected to occur (van der Spoel and Heyman, 1983; Angel, 1997).

The North Equatorial Current

The NEC crosses the central North Atlantic Gyral Province and enters the Caribbean basins through the channels between the Antilles, so feeding the Caribbean Current and closing the anticyclonic recirculation. The zonal band named by Longhurst (1998b) as NATR, is the most oligotrophic region of the North Atlantic. The author mentions that this province is less surveyed, in term of physical oceanography, than the adjacent provinces, and that is also true for the biological point of view (see Fig. 4.3). Most stomiid species seems to be absent from the central NATR, while others (classified as *Tropical – Subtropical*, *Broadly Tropical*, and some as *Caribbean complex*) are relatively abundant at those latitudes. Species such as *Chauliodus sloani* and *Malacosteus niger* that are distributed from polar to equatorial waters (*Widespread*) avoid the central NATR, and the northern and the southern core regions are inter connected by relatively narrow corridors along the margins of the Caribbean and the Eastern Tropical Atlantic.

Evolutionary biogeography

Few conclusions can be reached about the evolutionary biogeography of the group. Firstly the subject needs a solid phylogenetic framework; secondly it needs to address the global assemblage of the group being studied (Johnson and Zahuranec, 1998). Moreover, unsuspected genetic divergences (cryptic species) may exist among "taxonomic species" and the lack of such information compromises any attempt to detect evolutionary trends. In addition there are only two palaeontological records tentatively assigned to Stomiidae (maybe partly because of the poorly calcified bones; see Chapter 5); so although the group is considered an ancient deep-sea assemblage (Andriashev, 1956) there are no chronological data about its evolutionary history. Therefore only speculations can be made based on the patterns observed today. Moreover, if speciation is followed by dispersal and subsequent adaptations to new environments, the contemporary patterns may either retain vestiges of the ancient patterns or totally mask them. Molecular studies like those of Miya and Nishida (1996, 1998, 2000) will be essential for future advances in Stomiidae evolutionary history.

As reported many wide spread species maintain disjunct North Atlantic populations (e.g. bi-subtropical; bi-polar, etc.). Those patterns are generally considered to be the result of glacial cycles splitting populations. The maximum peak of the last glaciation occurred at about 18,000 years ago when polar waters extended southwards to the latitudes of the Mediterranean Sea (McIntyre et al., 1976; Angel, 1979). Then subtropical species were likely to have been shifted southward and restricted to a narrow low latitudinal band. They may either have merged with the equatorial species or the strict equatorial species may have died out. It is known also that glacial periods were much more severe in the enclosed North Atlantic basin than in the other oceans (Briggs, 1995). If these assumptions are correct then the present-day strict equatorial species may either have colonised the new ecosystem that developed after the glacial period from other oceanic basins, or have recently speciated. Most of the strict

Equatorial North Atlantic species are Atlantic endemics belonging to *Eustomias*, a genus that apparently has a much higher speciation rate than other stomiids.

A classical example of the effects of the last glaciation is the relict population of *Borostomias antarcticus* that is trapped in the Mediterranean Sea. Perhaps too the existence of Eastern Tropical Atlantic meta-populations of some boreal species (e.g. *Melanostomias bartonbeani* and *Rhadinesthes decimus*) may be also relicts from that period. No phylogenetic studies on *Borostomias* have been conducted, but if *B. antarcticus* is considered the sister group of the other two species (*B. mononema* and *B. elucens*), a succession of glacial and interglacial eras might created the isolation of relict populations at the Eastern Atlantic and/or Caribbean slopes, which subsequently speciated. Again regions favourable for speciation will have been the western and eastern boundary regions of the Atlantic.

Table 6.1 Broad geographical distribution of North Atlantic Stomiidae species. E-WTRA: Eastern and Western Tropical (Equatorial) Atlantic provinces of Longhurst (1998); * species global distribution needs to be re-evaluated.

Patterns	**Sp. n**	**Sub-patterns and Species**
Total World Ocean (tentative)	269	See Chapter 5, Table 5.1; Appendix E
Total North Atlantic species	141	
North Atlantic endemic	45	*Astronesthes zharodi; A. cyclophotus; A. neopogon; Chauliodus danae; Stomias brevibarbatus; Chirostomias pliopterus; Leptostomias macropogon; Photonectes dinema; Melanostomias melanopogon; Grammatostomias flagellibarba; Bathophilus proximus; B. vaillanti; Eustomias monodactylus; E. decoratus; E. drechseli; E. radicifilis; E. bibulbosus; E. bituberatus; E. micraster; E. bimargaritatus; E. patulus; E. silvescens; E. triramis; E. binghami; E. borealis; E. paucifilis; E. dendriticus; E. insularum; E. globulifer; E. contiguus; E. dispar; E. hypopsilus; E. variabilis; E. digitatus; E. dubius; E. polyaster; E. schiffi; E. hulleyi; E. leptobolus; E. macrophthalmus; E. precarious; E. pyrifer; E. quadrifilis; E. xenobolus;*
North Atlantic E-WTRA endemic species	9	*Leptostomias bermudensis; L. longibarba; Eustomias kreffti; E. melanonema; E. longibarba; E. aequatorialis; E. lanceolatus; E. monoclonoides; E. intermedius;*
Atlantic endemic species	76	North Atlantic endemic (n=45), plus North Atlantic E-WTRA endemic (n=9), plus (n=22): *Astronesthes caulophorus; A. leucopogon; A. richardsoni; A. similis; A. atlanticus; A. macropogon; A. micropogon; Chauliodus schmidti; Stomias lampropeltis; Leptostomias analis; L. leptobolus; Photonectes leucospilus; Odontostomias masticopogon; O. micropogon; Melanostomias biseriatus; Eustomias simplex; E. filifer; E. tetranema; E. tension; E. obscurus; E. arborifer; E. brevibarbatus*
North Atlantic disjunct populations	36	Atlantic endemic (n=4): *Astronesthes leucopogon; Eustomias simplex; E. tetranema; E. tensioni;* Widespread 3 oceans (n=25): *Neonesthes capensis; Rhadinesthes decimus; Borostomias antarcticus; Stomias boa; Trigonolampa miriceps; Photonectes braueri; P. caerulescens; P. mirabilis; P. parvimanus; Melanostomias bartonbeani; M. macrophotus; Grammatostomias dentatus; Bathophilus longipinnis; B. schizochirus; Eustomias braueri; E. macrurus; E. melanostigma; E. bigelowi; E. macronema; E. satterleei; E. schmidti; E. monoclonus; Idiacanthus fasciola; Aristostomias lunifer; A. grimaldii;* North Atlantic and Pacific (n=5): *Photonectes gracilis; P. achirus; Melanostomias margaritifer; Bathophilus altipinnis; Eustomias achirus*;* Atlantic and Indian (n=2): *Leptostomias bilobatus; Melanostomias bartonbeani*;*

Table 6.1 (continuation)

Patterns:	**Sp. n**	**Sub-patterns and Species**
North Atlantic E-WTRA * disjunct	11	Atlantic endemic (n=2): *Astronesthes macropogon; A. micropogon;*
		Widespread 3 oceans (n=8): *Borostomias mononema; Stomias longibarbatus; Photonectes phyllopogon*; Melanostomias tentaculatus; Bathophilus nigerrimus; B. pawneei; Aristostomias tittmani; A. xenostoma;*
		Atlantic and Pacific (n=1): *Thysanactis dentex*
Doubtful North Atlantic discontinuous populations	10	Atlantic endemic (n=2): *Astronesthes similis; Leptostomias leptobolus*
		Widespread 3 oceans (n=9): *Leptostomias haplocaulus; L. gladiator; Photonectes margarita; Melanostomias melanops; M. valdiviae; Bathophilus digitatus; Grammatostomias circularis; Eustomias furcifer; E. intermedius*
		Atlantic and Pacific (n=1): *Leptostomias gracilis;*
Other distribution patterns:	17	Atlantic and Indian (n=3*): *Astronesthes niger*; Eustomias lipochirus; Grammatostomias circularis**
		Atlantic disjunct / widespread 3 oceans (n=8): *Borostomias elucens; Heterophotus ophistoma; Stomias affinis; Flagellostomias boureei; Melanostomias melanops; Eustomias enbarbatus; Eustomias fissibarbis; Malacosteus niger*; Photostomias guernei*; Pachystomias microdon*
		Atlantic / Pacific disjunct (n=1): *Bathophilus brevis*
		Continuous distribution / widespread 3 oceans (n=4): *Astronesthes gemmifer; Chauliodus sloani; Echiostoma barbatum; Aristostomias polydactylus*

Table 6.2 Relative abundance ([*n_spec*/*std_h*]*100) of stomiid species by Longhurst' (1998b) Provinces (*Lgh_P*) and Biomes (*Lgh_B*). The numbers in bold represent regions where species have relatively higher abundances. x are records not included in the computations. No. sp, No. spec and *Std_h*: number of species and specimens and standardised fishing effort per province and biome (see Fig 2.2 for provinces full names).

Lgh_B	**Trade Wind Biome**						**Total**	**Coastal**	**Westerly Winds Biome**					**Total**	**Coastal**	**Atlantic Polar Biome**			**Total**
Lgh_P	ETRA	WTRA	CARB	NATR	NATR E	NATR W		CNRY	NAST W	NAST E	GFST	NADR	MEDI		NWCS	SARC	ARCT	BPLR	
No sp	33	83	102	80	71	74	132	36	101	73	83	36	5	111	15	10	8	5	11
No. spec	728	2849	3928	1318	1387	1859	12069	772	11917	7458	13253	4215	1534	38377	942	126	240	28	394
Std_h	2026	6101	13103	1234	3733	3733	34498	1393	26809	19147	29246	17627	3434	96263	1111	2820	3811	787	7419
Neonesthes capensis		0.066	0.008	0.081	**0.107**	**0.193**	0.075	0.072	**0.209**	0.047	0.031	0.034		**0.083**					
Astronesthes caulophorus	**0.197**	**0.180**		0.081	**0.348**		**0.084**	**0.502**											
Astronesthes zharodi		**0.016**			**0.027**		**0.006**												
Astronesthes cyclophotus					**0.054**		0.006		**0.015**	**0.016**	0.003			**0.008**					
Astronesthes gemmifer		**0.262**	0.023	0.081	**0.241**	0.024	0.090		**0.313**	**0.287**	0.072	0.091		**0.183**		0.035			0.013
Astronesthes leucopogon		0.066		**0.567**	**0.241**	**0.205**	0.107		**0.269**	**0.172**	0.031	0.011		**0.121**	0.090				
Astronesthes neopogon					**0.054**	**0.096**	**0.029**		**0.045**	**0.052**	0.007			0.025					
Astronesthes niger	**2.369**	1.541	0.458	4.778	5.920	0.229	1.452	0.072	1.403	0.830	**2.407**	0.108		1.307					
Astronesthes richardsoni	**1.480**	**8.900**	0.206	**1.296**	**1.822**		**1.983**	0.144	0.019		0.003			0.006					
Astronesthes similis		0.049	**0.801**	**0.729**	0.027	0.096	**0.365**		0.123		0.140			0.077					
Astronesthes atlanticus	0.148	**2.180**	0.351	0.162	**1.125**	0.048	**0.667**		0.004	0.042				0.009					
Astronesthes macropogon	0.148	0.049	**0.603**		**0.643**	0.024	**0.322**	0.072	0.086	0.010	0.096			0.055	0.090				
Astronesthes micropogon	**0.296**	0.164	**0.282**	0.081	**0.616**		**0.223**		0.060	0.084	0.027			0.042					
Borostomias antarcticus										0.005	0.137	0.340	0.058	0.107	**2.610**	0.248	**0.945**	**1.016**	**0.687**
Borostomias elucens	**1.135**	**1.246**	0.023	0.162	0.241		**0.328**	**0.574**											
Borostomias mononema	**0.197**	0.016	**0.076**		**0.134**		**0.058**	**0.072**		0.016				0.003					
Heterophotus ophistoma	0.049	**1.885**	0.092	0.243	0.027	0.024	**0.388**		0.004		0.007			0.003					
Rhadinesthes decimus					**0.027**		0.003		0.007	**0.052**	0.003	**0.102**		**0.032**			**0.157**		**0.081**
Chauliodus sloani	1.431	8.458	6.075	1.944	2.197	0.639	4.348	7.896	6.393	5.750	**18.868**	6.201	**10.890**	**10.180**	**14.220**	0.815	1.050	0.635	0.917
Chauliodus schmidti	**3.800**	**1.426**		0.405	**2.732**		**0.786**	**12.993**											
Chauliodus danae		0.033	1.816	**13.930**	**15.483**	**8.952**	**5.023**	3.948	**10.079**	**10.890**	1.679	0.057		**5.493**	0.180				

Stomias brevibarbatus		0.016	0.023	0.243	0.321	**0.566**	0.191		**1.074**	**0.413**	0.168		0.175	**0.438**					
Stomias longibarbatus	**0.395**	**0.148**	**0.145**	**0.162**	**0.348**	0.084	**0.168**	0.072	0.116	0.089	0.034	0.011		0.062					
Stomias lampropeltis	**4.589**	0.508			1.125		0.481	**8.183**											
Stomias boa	**0.493**	0.033		0.081	**0.214**	0.024	0.067	**2.728**	2.637	6.581	**12.265**	**15.005**	**30.864**	**9.618**	**63.540**	2.340	3.516	0.889	2.790
Stomias affinis	**4.935**	**1.869**	**2.229**	**1.701**	**4.072**	0.048	**1.980**	**1.579**	0.131		0.137	0.011		0.080	0.090				
Chirostomias pliopterus		0.049	0.031		0.080	0.024	0.035		**0.313**	**0.230**	0.150	0.102		**0.197**		0.035			0.014
Trigonolampa miriceps		0.016					0.003		0.022	0.037	0.007	**0.244**		0.060		**0.425**	0.026		**0.175**
Thysanactis dentex	0.099	**2.065**	0.038	**0.972**			**0.420**				0.003			0.001					
Leptostomias bilobatus		0.033	**0.053**		**0.107**	0.036	**0.046**				0.014			0.004					
Leptostomias gladiator		0.033	0.076		**0.188**	0.036	0.064		**0.283**	**0.214**	0.123	0.074		**0.172**	**0.180**				
Leptostomias haplocaulus	**0.197**	**0.148**			**0.241**	0.012	**0.067**	**0.144**	0.019	0.047	0.010	0.034		0.024					
Leptostomias analis		**0.016**	0.008		**0.027**		**0.009**		0.007			**0.011**		0.004					
Leptostomias bermudensis		**0.115**	0.031		**0.054**		**0.038**		0.037					0.010					
Leptostomias gracilis	0.049	**0.148**	0.008	**0.324**	**0.080**		**0.052**												
Leptostomias leptobolus			**0.031**			0.012	**0.014**		0.004	0.005				0.002					
Leptostomias longibarba		0.016	0.015	**0.081**	**0.027**		0.014			**0.057**	0.014	0.011		**0.018**		0.035			0.014
Leptostomias macropogon		**0.082**					**0.014**		0.004	0.005				0.002					
Odontostomias micropogon	**0.790**						**0.046**	**5.025**											
Odontostomias masticopogon								**0.072**											
Flagellostomias boureei	**0.247**	**0.246**	0.092	**0.243**	**0.616**	0.012	**0.171**	**0.718**	0.157	0.157	0.072	**0.113**		**0.117**		**0.284**	0.026	**0.127**	0.135
Photonectes gracilis		**0.016**	**0.008**				**0.006**												
Photonectes braueri					**0.295**	**0.193**	**0.078**	0.072	**0.131**	**0.115**	0.010	0.017		0.065					
Photonectes dinema			0.008		0.054	0.048	0.020		**0.283**	0.026	0.021			**0.090**					
Photonectes leucospilus		0.049	**0.076**		**0.054**	0.024	0.049		**0.160**	0.010	0.017			**0.052**					
Photonectes achirus			**0.053**				**0.020**		0.004			0.006		0.002					
Photonectes caerulescens		**0.115**	**0.038**	**0.243**			**0.043**					0.006		0.001					
Photonectes mirabilis		**0.197**	**0.092**		**0.107**	0.012	**0.084**		0.026	0.010	0.065	0.006		0.030					
Photonectes phyllopogon		**0.131**	0.023				**0.032**				0.003			0.001					
Photonectes margarita		0.033	0.122		**0.321**	0.012	0.090	0.072	**0.399**	0.026	**0.233**	0.023		**0.191**	0.180				
Photonectes parvimanus			0.023	0.081	**0.107**	**0.157**	0.061		**0.216**	0.052	0.034			**0.081**					
Echiostoma barbatum		0.311	**2.145**	0.081	0.107	0.229	**0.939**		**0.630**	0.068	0.154			0.236					

Table 6.2 (continuation)

Lgh_B	Trade Wind Biome						Total	Coastal	Westerly Winds Biome					Total	Coastal	Atlantic Polar Biome			Total
Lgh_P	ETRA	WTRA	CARB	NATR	NATR E	NATR W		CNRY	NAST W	NAST E	GFST	NADR	MEDI		NWCS	SARC	ARCT	BPLR	
Melanostomias bartonbeani			0.015	0.162	**0.911**	0.036	0.119	0.072	**2.085**	0.115	**1.494**	0.391		**1.129**	0.720	0.142	0.026		0.067
Melanostomias biseriatus	0.049	0.131	0.130		**0.429**	**0.181**	**0.165**	**0.215**	0.104	0.052	0.065			0.059					
Melanostomias macrophotus		**0.082**	**0.107**		**0.268**		**0.084**		0.004	0.026		0.006		0.007					
Melanostomias margaritifer			**0.053**			**0.060**	**0.035**	**0.072**	0.019	0.005				0.006					
Melanostomias melanopogon		0.016	**0.084**	**0.324**	0.027	**0.120**	**0.078**		0.048		0.051			0.029					
Melanostomias melanops	0.099	**0.229**	**0.145**	0.081	0.027		**0.107**		**0.157**	0.026	0.034			0.059					
Melanostomias tentaculatus		**0.279**	**0.298**	0.162	0.670	0.157	**0.278**	0.072	0.078	0.120	0.085			0.072					
Melanostomias valdiviae		0.049	**0.122**	0.081	0.027	**0.181**	**0.104**		**0.101**	0.031	0.034	0.006		0.046					
Grammatostomias circularis	**0.049**		**0.053**			**0.036**	**0.032**		0.019	0.005	0.010			0.009					
Grammatostomias dentatus						**0.036**	0.009		**0.041**	0.010	0.014			**0.018**					
Grammatostomias flagellibarba			0.023	**0.081**		**0.060**	0.026		**0.034**	0.021	0.024	**0.040**		**0.028**					
Bathophilus altipinnis		**0.016**					0.003		**0.022**		0.010			**0.009**					
Bathophilus nigerrimus		**0.246**	0.061	0.081	**0.482**	0.024	**0.128**	**0.144**	0.034	0.037	0.003	0.034	**0.903**	0.056					
Bathophilus proximus									**0.011**					**0.003**					
Bathophilus longipinnis			0.053	**0.162**	**0.054**	**0.072**	**0.049**	0.072	**0.101**	**0.052**	0.038	0.006		**0.051**					
Bathophilus brevis		**0.115**		**0.081**	0.027		0.026	**0.072**	**0.142**	0.031	0.010			**0.049**					
Bathophilus pawneei	0.049	**0.721**	**1.412**	**0.810**	0.027	0.205	**0.748**	0.072	0.104	0.010	0.079			0.055					
Bathophilus digitatus		0.066	**0.206**		**0.107**	0.012	**0.104**	**0.359**	0.034	0.031	0.021			0.022					
Bathophilus schizochirus			**0.015**			**0.024**	**0.012**		0.004					0.001					
Bathophilus vaillanti			0.046	0.162	0.429	0.060	0.084	0.144	**1.481**	**1.833**	0.215	0.045		**0.851**	0.180				
Eustomias braueri			0.015	**0.081**		**0.169**	**0.049**		0.030	0.031	0.010			0.018					
Eustomias macrurus	**0.148**	**0.508**	0.046		0.027	0.024	**0.125**		0.034	0.005	0.007			0.012					
Eustomias parri			0.008				0.003		**0.026**		0.007			**0.009**					
Eustomias enbarbatus	0.049	**0.557**	0.107	**0.567**	**0.750**	0.157	**0.281**		0.157	0.010	0.044			0.059					
Eustomias simplex			0.023			**0.193**	**0.055**		**0.048**	0.026	0.014			0.023					
Eustomias filifer		0.033	0.053	**0.081**	**0.080**		0.038		**0.134**	0.068	0.058	0.017		**0.072**					
Eustomias monodactylus		0.016	**0.031**		**0.054**		**0.020**		0.011	0.010	0.003			0.006					

Eustomias tetranema									0.007	**0.146**				**0.031**					
Eustomias decoratus									**0.004**					**0.001**					
Eustomias drechseli									**0.004**					**0.001**					
Eustomias furcifer			**0.015**				**0.006**		**0.019**					**0.005**					
Eustomias radicifilis						**0.036**	0.009		**0.037**					**0.010**					
Eustomias tenisoni						**0.060**	**0.014**		0.004					0.001					
Eustomias obscurus		0.393	0.099	**1.701**	**1.848**	**1.241**	0.667	**0.861**	**1.059**	**2.079**	0.065			**0.728**					
Eustomias bibulbosus		0.016	0.038	**0.081**		0.024	0.026		**0.153**		0.034			**0.053**					
Eustomias bituberatus		**0.033**	**0.038**			0.024	**0.026**		0.004					0.001					
Eustomias micraster			**0.069**			0.012	**0.029**												
Eustomias arborifer		**0.246**	0.015	**0.081**			**0.052**												
Eustomias bimargaritatus			0.046	**0.081**	0.027	**0.229**	**0.078**		0.015					0.004					
Eustomias kreffti		**0.082**					**0.014**												
Eustomias melanonema	**0.099**	**0.098**		**0.162**	0.027		**0.032**												
Eustomias melanostigma		**0.082**	0.023	**0.081**	**0.080**		**0.035**		0.004	0.005				0.002					
Eustomias patulus			**x**		**0.027**		**0.003**												
Eustomias longibarba		**0.098**	**0.092**		0.027	0.024	**0.061**		0.030	0.031	0.003			0.016					
Eustomias bigelowi			0.069	**0.162**		**0.181**	**0.075**		0.048		0.007			0.016					
Eustomias silvescens			**0.008**				**0.003**												
Eustomias triramis			**0.023**	**0.081**			**0.012**												
Eustomias binghami			0.031			**0.446**	**0.119**		0.041	0.010				0.014					
Eustomias borealis									**0.022**		**0.010**			**0.009**					
Eustomias fissibarbis	**0.148**	0.049	**0.137**		0.054	**0.169**	**0.116**		0.034	0.005				0.010					
Eustomias lipochirus		**0.115**	0.008	**0.081**	**0.080**	0.024	**0.041**		0.037	0.016	0.003			0.015					
Eustomias macronema					**0.027**	0.012	0.006		**0.048**	**0.031**	0.007			**0.022**					
Eustomias paucifilis			**0.038**	**0.162**		**0.072**	**0.038**		0.011		0.003			0.004					
Eustomias satterleei			0.008	**0.081**	**0.027**		0.009		**0.034**		0.007			**0.011**					
Eustomias schmidti		**0.164**	**0.374**	**0.162**	0.080	0.012	**0.188**		0.078	0.104	0.065			0.062					
Eustomias dendriticus		**0.016**			**0.027**		**0.006**		0.004					0.001					
Eustomias lanceolatus		**0.016**					**0.003**												
Eustomias monoclonus		0.016	**0.069**				**0.029**												
Eustomias achirus			0.015		**0.054**		**0.012**		0.004	0.005	0.003			0.003					
Eustomias aequatorialis	**0.148**	**0.066**					**0.020**												

Table 6.2 (continuation)

Lgh_B	**Trade Wind Biome**						**Total**	**Coastal**	**Westerly Winds Biome**					**Total**	**Coastal**	**Atlantic Polar Biome**			**Total**
Lgh_P	ETRA	WTRA	CARB	NATR	NATR E	NATR W		CNRY	NAST W	NAST E	GFST	NADR	MEDI		NWCS	SARC	ARCT	BPLR	
Eustomias insularum					**0.107**		**0.012**												
Eustomias intermedius		**0.016**					**0.003**												
Eustomias brevibarbatus		**0.328**	**0.259**	0.162		0.012	**0.165**		0.004					0.001					
Eustomias contiguus						**0.024**	0.006		**0.041**	0.010				**0.014**					
Eustomias dispar		**0.016**					**0.003**												
Eustomias hypopsilus			**0.267**				**0.101**												
Eustomias variabilis		0.016	**0.214**				**0.084**				0.003			0.001					
Eustomias digitatus			**0.023**				**0.009**		0.004					0.001					
Eustomias dubius			**0.015**	**0.081**			**0.009**		**0.011**		0.007			0.005					
Eustomias polyaster			**0.099**			0.012	**0.041**				0.007			0.002					
Eustomias schiffi									**0.067**		**0.031**			**0.028**					
Eustomias hulleyi			0.008			**0.096**	**0.026**		0.007					0.002					
Eustomias leptobolus			**0.015**				**0.006**												
Eustomias macrophthalmus			**0.053**			**0.072**	**0.038**												
Eustomias precarius			**0.008**				**0.003**												
Eustomias pyrifer			**0.008**				**0.003**												
Eustomias quadrifilis											**0.003**			**0.001**					
Eustomias xenobolus			**0.023**			**0.012**	**0.012**												
Idiacanthus fasciola		0.311	1.366	**2.592**	**4.527**	**2.386**	**1.731**	0.574	**2.335**	**2.382**	0.636	0.028		1.322	0.090				
Aristostomias lunifer			0.061	0.081		**0.217**	**0.078**		**0.142**	0.016	0.021			0.049					
Aristostomias tittmani		**0.164**	0.114		0.027		0.075		**0.328**	0.063	**0.150**	0.023		**0.154**	**0.450**				
Aristostomias grimaldii		**0.049**	**0.076**	**0.081**	0.027	0.024	**0.049**		**0.078**	0.026	0.038			0.038					
Aristostomias xenostoma	**1.234**	**1.147**	0.343	**0.648**	**0.455**		**0.478**		0.019	0.010	0.007			0.009					
Aristostomias polydactylus			**0.160**	**0.243**	**0.161**	0.024	**0.093**	**0.215**	0.056		0.048			0.030					
Malacosteus niger	0.987	**2.000**	0.275	0.081	**0.643**	0.181	**0.632**	**3.517**	**0.981**	0.439	**0.742**	0.204		**0.623**	0.090	0.035	**0.525**	**0.889**	0.377
Photostomias guernei	**2.319**	1.082	**3.076**	1.620	1.929	**2.229**	**2.299**	0.287	**3.898**	**2.930**	1.874	0.136		**2.263**	0.270				
Pachystomias microdon	**0.099**	**0.164**	0.015		**0.054**		**0.046**	**0.215**	**0.097**	0.010	0.027	0.028		0.043					

Table 6.3 Biogeographic pattern and sub-patterns of North Atlantic stomiid fish. n: number of species; (%) percentage in relation to total number of species; n= 141); Avg *Lgh_P*: average number of Longhurst provinces where the species occur; End.: number of North Atlantic endemic species; Disj: number of species that maintain disjunct North Atlantic (southward to equatorial waters) populations.

Pattern	**n (%)**	**Avg *Lgh_P***	**Sub-pattern**	**n**	**End.**	**Disj.**	***Species***
Equatorial	16 (11.3)	4.9		1		1	***Eustomias macrurus***
			Eastern Tropical - Caribbean	2		1	***Astronesthes richardsoni; Aristostomias xenostoma***
			West	5	1	3	***Thysanactis dentex; E. arborifer; E. krefjti; E. intermedius E. dispar***
			West - Caribbean	1			***Heterophotus ophistoma***
			West - Caribbean (distant neritic)	4		3	***Photonectes gracilis; P. caerulescens; P. phyllopogon; Eustomias brevibarbatus***
			West - Eastern Tropical - Caribbean	3		2	***Astronesthes atlanticus; Photonectes mirabilis; Eustomias melanostigma***
Equatorial complex	6 (4.3)	7.3	Equatorial (east) - Eastern tropical / Subtropical (west)	2			***Eustomias lipochirus; Pachystomias microdon***
			Equatorial (west) - Caribbean / Subtropical (west) / Eastern tropical - Equatorial (east)	1			***Melanostomias melanops***
			Equatorial (west) - Eastern Tropical - Western Tropical	1			***Eustomias enbarbatus***
			Equatorial (west) / Caribbean / Subtropical	1		1	***Eustomias longibarba***
			Equatorial (west) / Eastern tropical / Subtropical (west)	1	1		***Eustomias dendriticus***
Eastern Tropical - Equatorial	14 (9.9)	2.9		1	1	1	***Astronesthes zharodi***
			East; large range (distant neritic)	4			***Astronesthes caulophorus; Chauliodus schmidti; Stomias lampropeltis; Odontostomias micropogon***
			Eastern Tropical; limited range (distant neritic)	3	2		***Odontostomias masticopogon; Eustomias patulus; E. insularum***
			Equatorial (east)	3		2	***Eustomias lanceolatus; E. aequatorialis; E. monoclonoides***
			East - (distant neritic)	1			***Borostomias elucens***
			East; limited range (distant neritic)	2		2	***Leptostomias gracilis; Eustomias melanonema***
Eastern Tropical complex	2 (1.4)	5.5	Eastern tropical / Caribbean - Subtropical	1	1		***Eustomias monodactylus***
			Eastern tropical / Subtropical (west)	1		1	***Eustomias achirus***
Caribbean (distant neritic)	13 (9.2)	2			11	2	***Photonectes achirus; Eustomias bituberatus; E. micraster; E. silvescens; E. monoclonus; E. hypopsilus; E. variabilis; E. digitatus; E. polyester; E. leptobolus; E. precarious; E. pyrifer; E. xenobolus***

Caribbean complex	8 (5.7)	6.2	Caribbean – Equatorial (west) – Subtropical	1		1	***Eustomias schmidti***
			Caribbean – Tropical (west) – Equatorial (west)	1		1	***Bathophilus pawneei***
			Caribbean – Tropical (west) (distant neritic)	1	1		***Eustomias triramis***
			Caribbean – Tropical Gyre	1	1		***Eustomias paucifilis***
			Caribbean – Tropical Gyre – Subtropical (west)	1			***Grammatostomias circularis***
			Caribbean – Tropical Gyre – Subtropical (west) / Equatorial (west)	1			***Echiostoma barbatum***
			Caribbean – Western Tropical	1		1	***Astronesthes similis***
			Caribbean / Subtropical (west)	1	1		***Eustomias dubius***
Amphi-Atlantic (distant neritic)	8 (5.7)	7.6	Tropical	3		2	***Leptostomias bilobatus; Bathophilus digitatus; Aristostomias polydactylus***
			Tropical – Equatorial (east)	4		3	***Astronesthes macropogon; A. Micropogon; Borostomias mononema; Stomias affinis***
			Tropical – Equatorial (west)	1		1	***Melanostomias macrophotus***
Tropical – Equatorial	2 (1.4)	8	Northern Tropical – Caribbean / Equatorial	1			***Eustomias fissibarbis***
			Northern Tropical – Caribbean / Equatorial (west)	1		1	***Melanostomias tentaculatus***
Western Tropical Gyre	4 (2.8)	3			2	2	***Bathophilus schizochirus; Eustomias □ontigu; E. binghami; E. hulleyi***
Western Tropical Gyre complex	12 (8.5)	5.7	Tropical Gyre – Caribbean	3	2	1	***Melanostomias margaritifer; Eustomias bimargaritatus; E. Macrophthalmus***
			Tropical Gyre – Caribbean – Subtropical (west)	2		2	***Aristostomias lunifer; Melanostomias valdiviae***
			Tropical Gyre – Subtropical	1	1		***Astronesthes neopogon***
			Tropical Gyre – Subtropical / Boreal (east)	1	1		***Grammatostomias flagellibarba***
			Tropical Gyre – Subtropical – Eastern tropical	1		1	***Photonectes braueri***
			Tropical Gyre – Subtropical (west)	3	1	2	***Melanostomias melanopogon; Eustomias simplex; E. Bigelowi***
			Tropical Gyre / Subtropical (east)	1		1	***Eustomias braueri***
Tropical – Subtropical	3 (2.1)	10			1	2	***Chauliodus danae; Bathophilus longipinnis; Idiacanthus fasciola***
Broadly Tropical	1 (0.7)	11				1	***Stomias longibarbatus***
Subtropical	19 (13.5)	3.6		2	1	1	***Bathophilus vaillanti; Eustomias macronema***
			East	2	1	1	***Astronesthes cyclophotus; Eustomias tetranema***
			West	13	10	3	***Photonectes dinema; Bathophilus altipinnis; B. proximus; Eustomias parri; E. decoratus; E. drechseli; E. furcifer; E. radicifilis; E. bibulbosus; E. borealis; E. satterleei; E. □ontiguous; E. schiffi***
			West – Tropical Gyre	2		2	***Photonectes parvimanus; Grammatostomias dentatus***

Pattern	**n (%)**	**Avg Lgh_P**	**Sub-pattern**	**n**	**End.**	**Disj.**	***Species***
Subtropical complex	16 (11.3)	9.2	Subtropical – Eastern tropical	3		3	***Astronesthes leucopogon; Leptostomias gladiator; Eustomias filifer***
			Subtropical – Eastern tropical - Equatorial (east)	1			***Astronesthes gemmifer***
			Subtropical - Northern Tropical - Eastern tropical	1			***Eustomias obscurus***
			Subtropical - Tropical Gyre - Eastern tropical	2	1	1	***Neonesthes capensis; Stomias brevibarbatus***
			Subtropical (west) / Eastern tropical	2		1	***Photonectes leucospilus; P. margarita***
			Subtropical (west) / Eastern tropical - Equatorial (east)	1			***Bathophilus brevis***
			Subtropical - Boreal	1	1		***Chirostomias pliopterus***
			Subtropical - Boreal - Eastern Tropical	1		1	***Melanostomias bartonbeani***
			Subtropical - Boreal (east) / Eastern Tropical - Equatorial	1			***Flagellostomias boureei***
			Subtropical (west) - Boreal (west) / Equatorial (west)	1		1	***Aristostomias tittmanni***
			Subtropical (west) - Caribbean - Equatorial (west)	1		1	***Aristostomias grimaldii***
			Subtropical (west) - Caribbean / Equatorial (west) / Eastern tropical	1			***Melanostomias biseriatus***
Extended Eastern	2 (1.4)	7.5	Equatorial - Tropical - Subtropical	1		1	***Leptostomias haplocaulus***
			Polar - Eastern Tropical	1		1	***Rhadinesthes decimus***
Mediterranean - Extended Eastern	1 (0.7)	11				1	***Bathophilus nigerrimus***
Mediterranean - Eastern Tropical	1 (0.7)	6				1	***Stomias boa boa***
Boreal	2 (1.4)	4	East	1		1	***Trigonolampa miriceps***
			West	1	1		***Eustomias quadrifilis***
Boreal - Subtropical (east)	1 (0.7)	10		1	1		***Stomias boa ferox***
Polar - Boreal / Mediterranean (west)	1 (0.7)	8				1	***Borostomias antarcticus***
Widespread (anti-central)	2 (1.4)	15.5		2			***Chauliodus sloani; Malacosteus niger***

Chapter 7 - Biodiversity (and species assemblages) of North Atlantic Stomiidae

Introduction

Describing and understanding current biodiversity are major concerns for the scientific community and for the society in general. The recognition that understanding, cataloguing and maintaining biodiversity is a priority was made by the UNEP Convention on Biological Diversity and the subsequent treatise on Global Biodiversity Assessment (Heywood and Watson, 1995). The interest was, and still is, driven by awareness of the escalating erosion of natural ecosystems by the human societies; the objective is the conservation of the biological diversity and sustaining the global environment. Naturally, terrestrial biodiversity is better understood than marine biodiversity. However, well publicised marine research along with large-scale international initiatives (e.g. Census of Marine Life pilot projects [www.coml.or; Ausubel, 1999]), have raised general awareness of marine biodiversity. For obvious reasons the attention of marine biologists is focused chiefly on coastal and distant neritic systems and the progress toward the understanding the oceanic biodiversity is slow. Within the oceanic realm, biodiversity studies are focused mainly on the benthic ecosystems (see for example Ormond et al., 1997).

Information on pelagic diversity, and especially that concerning the midwater environment, is available primarily from approaches that are biogeographically oriented and fragmentary. Angel (1993, 1996, 1997), McGowan and Walker (1993) and Pierrot-Bults (1997) reviewed pelagic biodiversity issues. Apart from important theoretical generalizations, about the complexity and functioning of the domain, the empirical data are scarce. Angel (1993, 1997) illustrated horizontal and vertical patterns in pelagic biodiversity using data from the eastern North Atlantic collected by the former IOS along a (20ºW) latitudinal transects. Pierrot-Bults (1997) presented low-resolution global scale data on some taxonomic groups of pelagic invertebrates (Chaetognats, Pteropods and Euphausiids). The global distribution of Euphausiidae, compiled by Reid et al., (1978), was used by the authors.

Van der Spoel (1994d) constructed a hierarchical system of biodiversity indices to measure total pelagic biodiversity (taxonomic, ecological, genetic historical and phylogenetic). However, few empirical data were provided and the author recognised that published data are very sparse partly because pelagic biodiversity is a widely neglected subject and taxonomic expertise and competence is rare. The method was seldom applied to real data.

Most of large-scale pelagic biodiversity approaches focused on planktonic invertebrates. Studies on micronektonic midwater fish are rare. Probably Marshall (1963) was the first to tackle the subject More recent contributions include: Cohen (1986) who analysed a collection of fish fauna made along a latitudinal transect across the Indian Ocean; Haedrich (1985) who calculated species-areas relationships (for Myctophidae in Backus et al. [1977] provinces), corrected by a productivity factor; Badcock and Merrett (1977) and Angel (1993) who presented a profile of the number of midwater fish species along a latitudinal transect along the Northeast Atlantic; van der Spoel (1994d) who computed some relationships for distribution of within-group diversity of Myctophidae. Other authors (e.g. Backus et al., 1977; Themelis, 1996) employed biodiversity methodologies (e.g., the Shannon index; species-areas and rarefaction curves, etc.) to study regional faunas in boundary regions.

At the global scale, pelagic diversity at the species level is very low, with many species apparently spread throughout several oceanic basins (Van der Spoel and Heyman, 1983). Conversely, local pelagic diversity is high (i.e. includes many species of the total inventory), even compared with adjacent neritic systems. However, high variability is reported at small time/space scales because of the dynamic nature of the realm.

Widespread species are expected to have high infra-species genetic diversity (Pierrot-Bults, 1998b), and many cryptic species are expected to exist (e.g. Miya and Nishida, 1997, 2000). Nevertheless, the rate of speciation is considered low, reflecting the permeability of the boundaries and consequent gene flow.

Species diversity is lowest at high latitudes, higher at middle latitudes and intermediate diversity at the equatorial belt (Reid et al., 1978). The North Atlantic northward from ca. 40ºN maintains relatively low diversity communities driven by a seasonally pulsed high production (primary and secondary) cycle (e.g. Longhurst, 1998b). At the other extreme, the permanently stratified tropical water column with a more steady cycle of (low) productivity, maintains higher levels of biological diversity (species richness and evenness). Others (e.g. Badcock and Merret, 1977; Angel, 1993, 1997) have reported high diversity at frontal zones of Central South Atlantic and North Atlantic water (i.e. the Cape Verde Frontal Zone).

Objectives of the chapter

1. To contribute to a better understanding of patterns of pelagic biodiversity in the North Atlantic, using the stomiid fish species as an example; 2. to identify the taxonomic composition and structure of the total Stomiidae assemblage; 3. to evaluate the potential of available data to assess the geographic distribution of biodiversity properties; 4. to describe and compare the diversity patterns of regional stomiid assemblages; 5. to discuss the basin-scale distribution of the observed pelagic biodiversity.

Material and Methods

Data

The raw data used are presented in Chapter 2. The method for biomass estimation is presented in Chapters 2. The calculations of the standardised sampling effort (*std_h*) were detailed in Chapter 4. The taxonomy and the biology of this fish family are presented in Chapter 5.

These analyses include only records associated to net-hauls with information on sampling effort (see Chapter 4) and occurrences identified to species level. This sub-sample contains all the Stomiidae species reported in the North Atlantic except *Eustomias monoclonoides*, which is known only from two records in the eastern Gulf of Guinea.

Spatial arrangement of the data

The grid formed by 5º per 5º latitude/longitude squares (*sq_5x5*) was used for spatial locations (Fig. 2.2). Standardised data on sampling effort and total numbers (and estimated weight) of specimens per species were pooled from all net-hauls carried out within a *sq_5x5*. The Longhurst's system was superimposed on the *sq_5x5* grid and used as an ecological/ biogeographic grouping factor. When the boundaries of the system crossover and split a latitudinal or a longitudinal band of *sq_5x5*, those were sub-divided and the net-hauls carried inside each part were pooled. This practice allowed the correction of biogeographic information, but in poorly sampled regions it weakened the local resolution of the data. The number of sub-divided *sq_5x5* is indicated by the notation *sq_5x5 (n+)*. Every net-haul was also classified according the Longhurst's (1998b) system.

Data matrices

Matrices of species relative abundance (number of fish caught per standard hour of fishing; *no_spec*/*std_h* * 100) and estimated biomass (g/*std_h*) per *sq_5x5* and *Lgh_P* were assembled. They were obtained by pooling standardized fishing effort, species numbers and biomass from net-hauls associated with each spatial unity. Matrices on absolute numbers of specimens per species per *sq_5x5* and *Lgh_P* were used to compute the saturation curves (see Appendix G).

Species abundance-biomass relationships

The species relative abundance-biomass curves (ABC) were computed for every province (Appendix G). Based on the relative position of the abundance and biomass curves, the W statistics were computed (values range -1 to 1, positive when the sample is biomass dominated [Clarke and Warwick 1994]). The relationship between both curves is thought to reflect, the level of disturbance an assemblage of species faces (originally pollution; Clarke and Warwick, 1994) and under "undisturbed" conditions W assumes a positive value. Values around 0 are expected for moderated disturbed conditions.

Abundance categories

Plots of geometric abundances classes were computed for every Longhurst province. (Appendix G). They represent the abundance structure of the community but they are hardly compared because they were built on matrices of numbers of specimens per species. So, rare species may distribute in the first and second classes in the less well sampled provinces but spread out across three or four classes in heavily sampled provinces. To resolve this problem the species were classified in abundance categories based on their relative abundance. The criteria adopted were based on the interpretation of the effort needed to sample one specimen of a hypothetical species that occurred at given abundance. Arbitrarily rare species were considered those that had relative abundances smaller or equal to 0.08 *no_spec/std_h*; moderate species between 0.09 and

1.5 *no_spec/std_h*; and abundant species had relative abundances higher than 1.5 *no_spec/ std_h*.

Biodiversity indices

Each biodiversity index characterises the community structure in a different perspective. Often indices are used in combination when comparisons between assemblages biodiversity are intended. Ten biodiversity indices were calculated over the matrices of species numbers, relative abundances and biomass per unit area and province. Apart from the observed number of species (S), they were considered in three groups:

1) Standard. H': Shannon-Wiener diversity (base e); J': Pielou's evenness; d: species richness (Margalef); 1-λ': Simpson's dominance;

2) Hill's numbers. N1; N2; and N∞;

3) Taxonomic and phylogenetic. Δ^+: average taxonomic distinctness; Λ^+: variation on taxonomic distinctness; Φ^+: average phylogenetic diversity.

Standard indices and Hill's numbers are widely used in empirical biodiversity approaches and discussed in many reviews of biodiversity methodologies (e.g. Magurran, 1988; Heip et al., 1998; Southwood and Henderson, 2000). The actual formulas used are those presented in Clarke and Warwick (1994) and in the PRIMER-E v.5 manual and analysis package (Clarke and Gorley, 2001).

The taxonomic and phylogenetic indices (Clarke and Warwick, 1998, 2001; Clarke and Gorley, 2001) intend to measure the taxonomic relatedness of species from an assemblage. They measure the distances linking species of a sample, through a hierarchical taxonomic system (see taxonomic trees files below), and compare it with a master list of regional (provincial) species. The taxonomic diversity index (Δ) applies to relative abundance data and is considered a generalized case of the Simpson's index, incorporating a component of taxonomic relatedness. The index was found to be dependent of species abundance distribution and Clarke and Warwick (1998) created the average taxonomic distinctness index (Δ+), which applies the same principle to presence/absence data. It is calculated by summing the path lengths across a taxonomic tree between pairs of species (total taxonomic distinctness; SΔ+) divided by the numbers of paths. Clarke and Warwick (1998) proved that Δ+ is independent of sampling size (effort). The variation in taxonomic distinctness index (Λ+; Clarke and

Warwick, 2001) quantifies the variability between distances that account for the Δ+. It is also applicable to presence/absence and is quoted to give new insights on the diversity structure of the assemblages. Δ+ and Λ+ were viewed as complementary because they varied independently. Total phylogenetic diversity (SΦ+) was defined as the total length in a taxonomic tree, which is greatly dependent of the number of species observed. Dividing SΦ+ by the number of species, Clarke and Warwick (2001) derived the average phylogenetic diversity (Φ+) that is expected to be less dependent of sampling effort and then of the observed number of species.

Preliminary analyses showed that Δ matches the Simpson's index (Pearson coefficient = 0.98) and SΔ+ and SΦ+ are highly correlated with the observed number of species (Pearson coefficient = 0.998 and 0.997, respectively). Consequently the indices do not bring into the analysis any novelty value, particularity of the community, and therefore they were not used in this study.

The taxonomic trees files

The faunistic inventories used to calculate the taxonomic indices selected were based on the Stomiidae systematics discussed in Chapter 5. Ideally those taxonomic lists would reflect the phylogeny of the species involved. The stomiids were organized in sub-families and genera according the Fink's (1985) classification. A constant increment between steps in the taxonomic tree hierarchy was assumed.

Local versus regional diversity

The species sampled inside a province were considered to represent the assemblage of species of that province. The inventory was treated as the regional (provincial) assemblage at species level and the regional diversity properties (coded by the biodiversity index followed by R) were calculated on matrices of species relative abundance or absolute values (R n) and biomass (R w) per Longhurst provinces. The diversity properties found in a *sq_5x5* were considered to represent the local diversity. The average local diversity indices within a province (coded by the biodiversity indices acronyms followed by L) were computed using the values obtained from the *sq_5x5* (n+) classified under that province (see Appendix G).

The geographical distribution of selected local (*sq_5x5*) biodiversity properties has been mapped. Data kriging was the geostatistical gridding method used to interpolate data obtained from each *sq_5x5* (n+) (see Chapter 6 for methods).

Multivariate statistics

The multivariate statistical procedures (classification and ordination) followed the strategy described by Field et al. (1982), detailed by Clarke and Warwick (1994) and adopted in the ecological package PRIMER-E (Clarke and Gorley, 2001). The raw data were subjected to a square root transformation and the Bray-Curtis similarity measure was used to compute the triangular similarity matrix. Cluster analysis used group average linkage. The same matrix was also used to produce multi-dimensional scaling (MDS) analyses.

Results

The stomiids constitute the most speciose midwater fish family that live in the North Atlantic with at least 141 species. The highest numbers of species were sampled in the Caribbean and Gulf of Mexico (CARB) and in the western sector of the North Atlantic Subtropical belt (NAST W) (102 and 101, respectively). A considerable number of species were also caught in the western equatorial province (WTRA), in the Slope Water off Canada (GFST) and in the Eastern Tropical Atlantic (83, 83 and 80, respectively). Important numbers of stomiid species were observed in NATR W (74), NAST E (73) and NATR (60). The provinces NADR, CNRY and ETRA had considerably lower species richness (36, 36 and 33, respectively), but much higher than the northern regions (NWCS, SARC, ARCT, and BPLR) and the Mediterranean Sea (MEDI). However, the number of species reported to those regions is certainly dependent of the sampling effort.

How well sampled were the Longhurst (1998b) provinces?

Judging from the species-area cumulative curves obtained for each province (Appendix G) it is apparent that ETRA, NATR, CNRY, NWCS and NATR E have not been sufficiently studied and that more species can be expected to be found with more sampling. Although more thoroughly surveyed, the faunas of SARC and WTRA are likely to be slightly augmented also by further sampling. The asymptotic phase of the curve has almost been reached for the remaining provinces. These observations were supported by the slope of the logarithmic function of the curves.

The picture obtained from the rarefaction curves (Appendix G) is similar. Though no true asymptotic curve was obtained from any of the provinces, the differences between the NAST W, GFST, NADR, NAST E and MEDI, and at the other extreme, NATR, CNRY, ETRA, NATR E, NWCS and SARC (where more species are expected if numbers of specimens increase) are evident. An intermediate rate of recruitment of new species may be expected from NATR W, WTRA and CARB.

Fishing effort and number of species

From the relationship between fishing effort and the observed number of species (S) (Fig. 7.1) it is apparent that a relatively reduced effort produced a significant number of species at NATR, CNRY, NATR E and ETRA, which were otherwise considered to be undersampled provinces. The ratio was relatively high also for WTRA and NWCS decreasing progressively toward the more intensively studied regions (GFST, NAST W, NAST E and NADR). The polar provinces (SARC, ARCT and BPLR) and the Mediterranean Sea (MEDI) also had low values of the ratio between the sampling effort and number of species reflecting the smaller species inventories in those regions. Although the scatter plot of sampling effort versus number of species shows a trend for a logarithmic distribution, there is no inter dependence between these two variables (Pearson coefficient = 0.45).

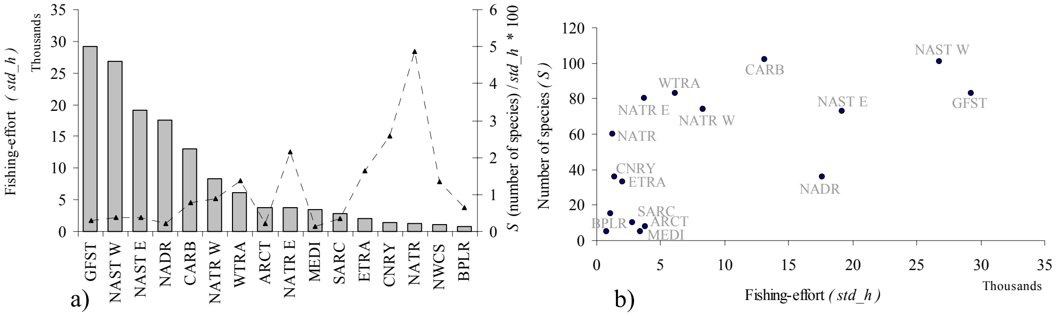


Figure 7.1 Relationships between fishing effort (*std_h*) and total number of species (S) per Longhurst's (1998b) provinces. a) fishing effort: columns (primary y-axis); number of species per fishing effort: triangles (secondary y-axis); b) number of species per fishing effort (see Fig. 2.2 for provinces acronyms).

Abundance-Biomass-curves

Dominance of the most abundant species (i.e. rank 1 in number of specimens) was less pronounced at ETRA, WTRA, CARB, NAST W, CNRY, NATR E, BPLR and NAST E (up to 30%) than it was for GFST, SARC, ARCT, NADR, MEDI and NWCS (44% - 77%) (Appendix G). NATR and NATR W reached intermediate values between those two groups of provinces. The figures were similar when the three most abundant species were considered: CARB, WTRA, ETRA and NATR E had lower dominance levels (42% - 47%) and GFST, BPLR, SARC, ARCT, NADR, NWCS and MEDI showed high dominance levels (78% - 99%).

In terms of biomass the differences between provinces were greater than for abundances. The regions showing a more even distribution were NATR E, WTRA, NATR W, NATR, NAST W and ETRA (13% - 23%), while CARB, MEDI, GFST, NADR, NWCS and BPLR had the most dominated (uneven) assemblages (50% - 68%). Values for NAST E, SARC, CNRY and ARCT (33% - 39%) were intermediate.

The CARB assemblage showed the most marked difference between dominance in numbers and in biomass; abundances were even whereas in contrast biomass was highly dominated.

W statistics

The eastern equatorial and the tropical boundary provinces (ETRA, CARB and CNRY) reached the highest positive values of W (Fig. 7.2), whereas values for MEDI and

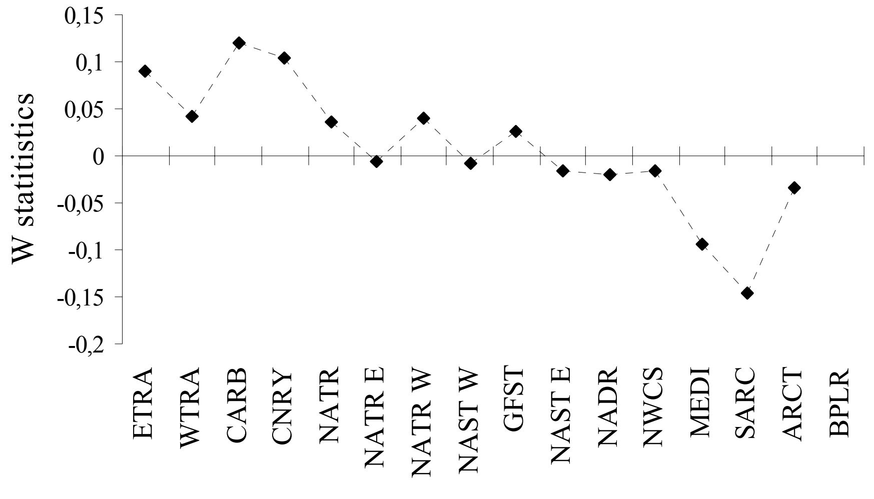


Figure 7.2 W statistics for the relationship between abundance and biomass dominance curves per Longhurst's (1998b) provinces (see ABC plots in Appendix G).

SARC were the lowest. It means that biomass curves lie above the abundance curves in the assemblages with high positive W values, but below in the Mediterranean and Sub-Arctic provinces. The remaining provinces attained values of W close to zero indicating that essentially both abundance and biomass curves overlie each other. However, even the extreme values of W of the CARB and SARC assemblages (e.g. 0.120 and -0.146) were far removed from the extreme limits of the statistics (i.e. -1, 1). The BPLR result (W = 0.483; not represented in Fig. 7.2) was probably influenced by the quality (both sparse and uneven) of the data available.

The geometric abundance classes

The number of classes in the geometric plots ranged between 13 for GFST, to 7 for ETRA and NWCS, and 5 to 3 for SARC, ARCT, BPLR and MEDI (Appendix G). As expected, most of the assemblages contained a relatively high number of rare species (i.e. the first geometric classes), then fewer species with intermediate numbers of specimens and by very few species represented by many individuals. However, a comparative analysis based on abundance classes (computed on numbers of specimens) may lead to erroneous conclusions, as different provinces were sampled at different intensities and that may have masked the true relative abundances of the species.

Abundance categories

In ETRA, CNRY, NATR E and NATR the geometric class 1 encompassed all the species considered rare (i.e. < 0.08 *no_spec*/*std_h*) (Table 7.1). As one moves toward the most intensely sampled provinces, rarer species become represented by more specimens and so shifted in subsequent classes. The mode of the geometric curve in those provinces was clearly extended and much smoother. Moderately abundant species (i.e. >0.08 and <1.5 *no_spec* /*std_h*) distributed along the next three to five classes of the geometric plots. The remaining classes included the few abundant species (i.e. >1.5 *no_spec* /*std_h*).

Table 7.1 Data on species relative abundance categories by Longhurst's (1998b) province (*Lgh_P*). Rare species: ≤ to 0.08 *no_spec/std_h*; moderately abundant species: ≥ 0.09 and ≤ 1.5 *no_spec/ std_h*; abundant species: > 1.5 *no_spec/std_h*. S: number of species reported for each province; cl (n): number of the geometric classes in the geometric abundance plots (see Appendix G); ab (avg): averaged relative abundance of species; sp (%): number of species (percentage); and spec (%): number of specimens (percentage); classified under each category.

Lgh_P	**S**	**rare**				**moderate**				**abundant**			
		cl (n)	**ab (avg)**	**sp (%)**	**spec (%)**	**cl (n)**	**ab (avg)**	**sp (%)**	**spec (%)**	**cl (n)**	**ab (avg)**	**sp (%)**	**spec (%)**
ETRA	33	1	0.05	18.2	1.0	4	0.49	66.7	35.8	2	3.39	15.2	63.1
WTRA	83	2	0.03	37.8	2.0	4	0.32	47.6	19.0	2	4.05	14.6	79.0
CARB	102	3	0.02	53.9	5.1	4	0.32	39.2	27.8	3	3.36	6.9	67.1
CNRY	36	1	0.07	38.9	1.9	3	0.41	38.9	9.8	4	6.25	22.2	88.3
NATR E	80	1	0.03	26.3	1.0	5	0.42	62.5	25.7	3	7.48	11.3	73.3
NATR	60	1	0.08	43.3	5.2	3	0.47	43.3	21.2	3	6.42	13.3	73.6
NATR W	74	3	0.03	60.8	6.6	4	0.54	35.1	30.9	2	5.63	4.1	62.5
NAST W	101	4	0.02	56.4	2.9	5	0.48	37.6	29.4	3	5.86	5.9	67.7
GFST	83	5	0.03	78.3	3.7	3	0.36	14.5	6.9	3	6.43	7.2	89.4
NAST E	73	4	0.03	69.9	3.5	4	0.40	20.5	9.4	4	5.52	9.6	87.0
NADR	36	4	0.03	66.7	2.3	3	0.25	27.8	7.8	2	10.60	5.6	89.9
NWCS	15	1	0.09	33.3	0.5	3	0.46	46.7	2.6	3	26.79	20.0	96.9
MEDI	5	1	0.06	20.0	0.1	2	0.54	40.0	2.5	2	20.88	40.0	97.4
SARC	10	1	0.04	40.0	3.2	3	0.46	50.0	43.5	1	2.34	10.0	53.2
ARCT	8	1	0.03	37.5	1.3	3	0.56	50.0	42.7	1	3.52	12.5	56.1
BPLR	5	0				3	0.65	100.0	100.0				

More even distributions between the abundance categories were found in the equatorial and eastern tropical provinces (ETRA, WTRA, CNRY, NATR E and NATR). Where a large percentage of the species occurred in moderate abundance (39% – 67%), followed by rare species (18% - 43%) and then by a significant proportion of relatively abundant species (11% - 22%).

The western tropical, the subtropical and eastern boreal provinces (i.e. CARB, NATR W, NAST W, NAST E and NADR) rare species were an important component (54% - 70%), moderately abundant species were intermediate (20% -39%), and less than 10% of species were dominant. The high proportion of rare species is more apparent in the GFST (78%) than in NADR and NAST E. The stomiid impoverished provinces (SARC, ARCT, NWCS and MEDI), showed an irregular pattern somewhat similar to that found for the eastern tropical provinces.

Rare species accounted for less than 6% of the total number of specimens in most provinces. Moderately abundant species contributed 19% to 36% of the individuals in the equatorial, tropical, western subtropical and polar provinces, and a strong numeric dominance (89% - 97%) by few species was evident in the remaining provinces.

Diversity indices

Species richness

Plots of biodiversity indices values per Longhurst's provinces are presented in Figure 7.3. As mentioned above, the observed number of species (S; regional diversity) was high in the western Atlantic tropical – subtropical provinces but low in the polar regions (and the Mediterranean) (Fig. 7.3a).

The number of specimens caught at the polar provinces (ARCT, BPLR and SARC) prevented the use of the rarefaction formula. When those provinces were excluded, the analysis was restricted by NATR sample size. For samples of 500 individuals the expected number of species was higher at CARB and NATR (63 species) followed by WTRA, NATR W, NATR E and NAST W (55 to 51 species). The NAST E ranked next before ETRA, GFST and CNRY, all with about the same numbers of species (32). NADR and NWCS showed a lower value of ES (500) (19 and 12 respectively) but clearly higher than MEDI (4 species). When the ES (2500) were considered only six provinces were available for comparisons. CARB was still the most species-rich province (96 species). WTRA and NAST W had values clearly higher (82 and 79, respectively) than those computed for NAST E and GFST (60 and 57). The lowest expected number of species was in NADR (31).

The Margalef's index (d) (Fig. 7.3e) showed CARB having the highest value of species richness, followed by NAST W. NATR W, WTRA, GFST, NATR, NAST E and NATR E ordered along a smooth decreasing gradient. NADR, ETRA and CNRY had much lower values of this index, but the lowest were for SARC, ARCT, BPLR and MEDI. In terms of biomass the index d assumed slightly lower values and the relative richness of CARB, NATR W and GFST (as SARC, ARCT and BPLR) were clearly reduced.

Diversity

H' and N1 (Fig. 7.3 b,f) arranged the provinces in a similar manner, differing only in relative differences between provinces. CARB got the highest value of both indices,

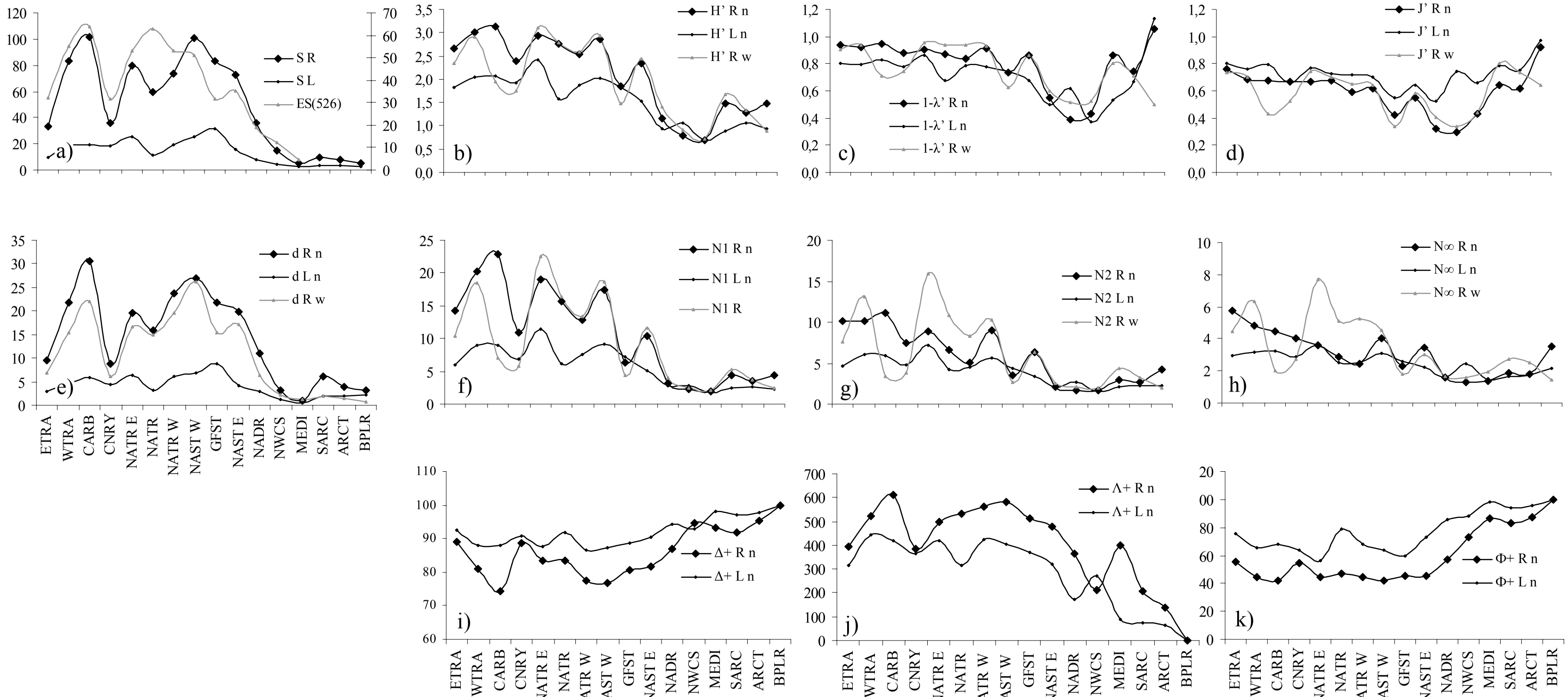


Figure 7.3 Distribution of biodiversity indices by North Atlantic Longhurst Provinces. Regional diversity (lines ◆ and ▲ coded by R after the indices acronyms); and averaged local diversity (lines • codified by L after the indices acronym); n (after L and R) – indices calculated on relative abundance (*n_spec/std_h*); w (after R) – indices calculated on relative biomass (*g/std_h*) (see text for more details). a) S: number of species; ES (526) rarefaction value (right axis); b) H': Shannon-Wiener diversity (base e); c) 1-λ': Simpson's dominance; d) J': Pielou's evenness; e) d: species richness (Margalef); f) – h) N1 - N∞: Hill's numbers; i) Δ^{+}: average taxonomic distinctness; j) Λ^{+}: variation in taxonomic distinctness; k) Φ^{+}: average phylogenetic diversity.

slightly higher than WTRA, NATR E and NAST W. A group of equatorial and tropical provinces (ETRA, NATR, NATR W), and then CNRY, NAST E and GFST followed. Polar provinces reached higher values of the indices than NADR, NWCS and MEDI. In terms of biomass the values reached by H' and N1 in NATR E and NAST W surpassed the values computed for CARB and WTRA assemblages. Diversity decreased at CNRY but it does essentially at CARB, which ranked closer to GFST conversely to the more diverse tropical provinces.

Equitability

The Pielou´s evenness index J' (Fig. 7.3d) decreased smoothly from the equator northward to the subtropical belt. ETRA had the highest value of the index followed by WTRA, CARB, NATR E, CNRY and NATR. Evenness was higher at NAST W than at NATR W and NAST E. Dominance was high in GFST and MEDI, but not as high as in NADR and NWCS. The J' increased again at the polar provinces, peaking in BPLR.

A similar pattern was depicted by the Simpson's index ($1-\lambda$) (Fig. 7.3c). However, in CARB and NAST W it showed a relative increase and attained values similar to those of the ETRA, WTRA and NATR E assemblages. The probability of sampling a specimen from the same species was lower at NAST E than at NATR W. Also the differences between GFST and NADR, NWCS and MEDI were more apparent.

Hill's numbers, N2 and $N\infty$ (Fig. 7.3g,h), indicated that CARB, ETRA and WTRA supports the more even and diverse assemblages, followed by NAST W, NATR E and CNRY. Conversely GFST, SARC, ARCT, NADR, MEDI and NWCS had more dominated assemblages, whereas both numbers on NATR, NAST E and NATR W were intermediate.

The obvious difference between the indices (i.e. N2, $N\infty$ and J', $1-\lambda$) was the relative positions of SARC, ARCT and BPLR, which ranked much lower (more dominated and less diverse) by the Hill's numbers.

In terms of biomass a similar pattern emerged. However, a conspicuous difference is that evenness decreased considerably at CARB and CNRY to values only slightly greater than those computed to NADR, GFST and NWCS. The J' and $1-\lambda$ indices peaked at SARC, but dominance in biomass increased clearly at BPLR. Hill's numbers computed over the matrix of biomass showed a higher range of variation and NATR E had the most even community.

Taxonomic diversity

The three taxonomic indices computed for each Longhurst provinces (regional diversity) correlated with the observed number of species (S) (Fig. 7.3i,j,k). The average taxonomic distinctness (Δ^+) and the average phylogenetic diversity (Φ^+) varied inversely with S (correlation coefficient: -0.96 and -0.91, respectively), while the variation in taxonomic distinctness (Λ^+) showed a positive relationship with S (correlation coefficient: 0.88). The polar regions and the other less diverse provinces (NWCS and MEDI) got higher values of Δ^+ and Φ^+. ETRA, NADR and CNRY followed. NATR E, NATR, NAST E and WTRA assumed intermediate values of the indices. The lowest values (more diverse) were computed for NATR W, NAST W and CARB. The inverse order was found when Λ^+ has been considered.

Averaged local diversity

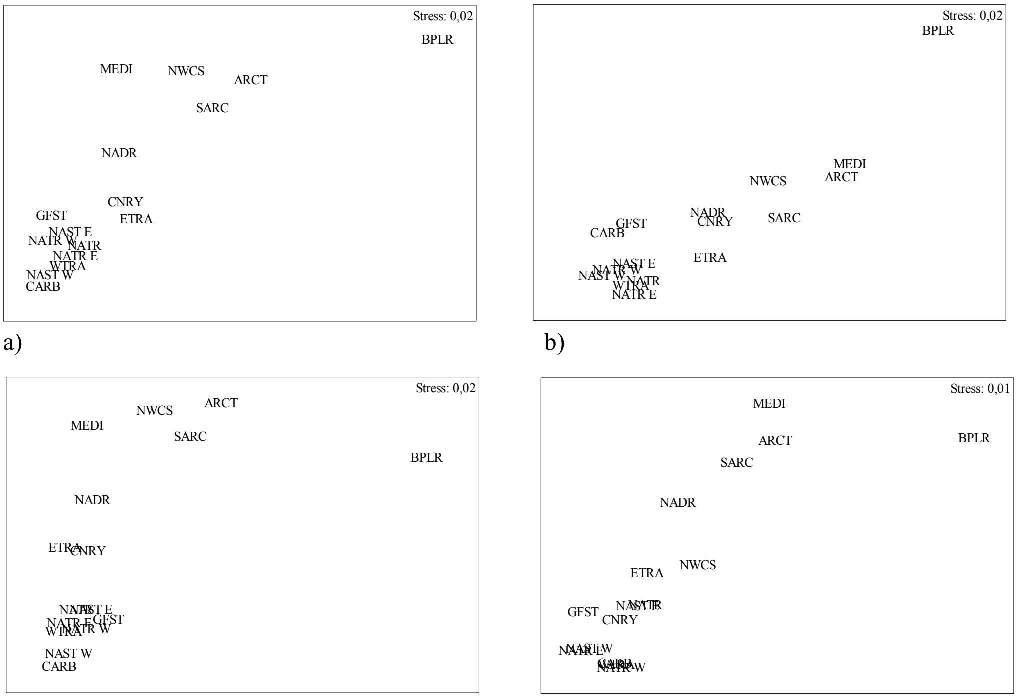
The local diversity indices (L), computed for each *sq_5x5* and averaged for the biogeographic provinces, were plotted along the regional diversity (Fig. 7.3; and Appendix G). The numbers for most of the averaged local diversity indices were lower than the values computed for regional diversity. The exceptions were J', Δ^+ and Φ^+, but as noted before both taxonomic indices varied inversely with the increasing diversity. The differences between the provinces noticed in the regional (provincial) diversity analysis were not as obvious when the averaged local diversity was considered because the indices assumed a more smooth distribution.

The main differences perceived between regional and local diversity were the relatively higher diversity reached by NATR E, GFST and NWCS (but also by CNRY, NATR W and ARCT), whereas the relative local diversity computed especially for CARB and NATR (but also for WTRA, NADR, SARC and NAST E) were much lower.

The general picture from the provincial taxonomic funnels computed for $\Delta+$ and $\Lambda+$ (see Appendix G) was that local (*sq_5x5* (n+)) taxonomic diversity was lower than that generated randomly from the regional pool of species (but often within the 95% tolerance limits of the computed regional means).

Classification and ordination of Longhurst provinces by biodiversity indices

The multivariate analyses computed on the entire set of biodiversity indices (11) that characterised each Longhurst province (Fig. 7.3) are summarised in Figure 7.4. The four MDS used different data matrices but all clearly separated BPLR from the other provinces. The stomiid impoverished ARCT, SARC, MEDI and NWCS fell between the BPLR and the more diverse provinces. NADR linked the northern and the broadly tropical provinces. In most plots, CNRY and ETRA were separated from the remaining warm water provinces as a result of their intermediate levels of diversity. The regions with high stomiid diversity grouped in the left corner of the plots opposite to BPLR. In the abundance and biomass plots, GFST was slightly closer to the provinces that show lower diversity and higher dominance. The remaining tropical and subtropical provinces were more or less amalgamated depending of the type of data used. In terms of biomass (Fig. 7.4b) CARB joined GFST and both separated from the more diverse provinces and CNRY grouped preferentially with NADR. In terms of absolute numbers (Fig. 7.4c) the pattern was similar to that of the regional diversity in abundance. In the MDS computed



a) b)

c) d)

Figure 7.4 Multidimensional scaling analyses (MDS) on the matrices of biodiversity indices computed for the North Atlantic Longhurst‘s provinces stomiid fish assemblages (Fig. 7.3; see Fig. 2.2 for province acronyms); a) relative abundance (*no_spec*/*std_h*) b) relative biomass (*g*/*std_h*); c) absolute abundance (*no_spec*); d) averaged local (*sq_5x5*) abundance.

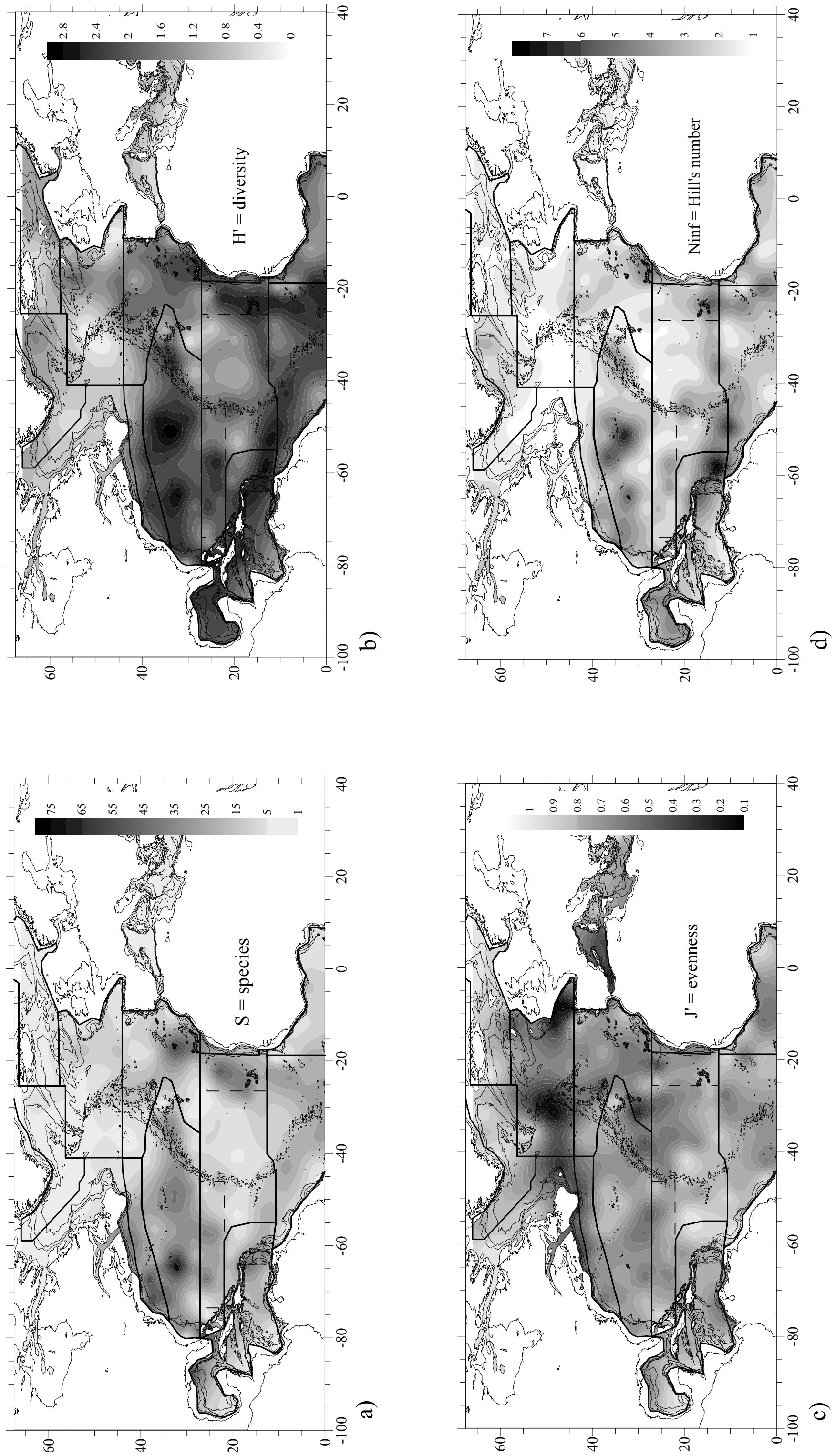
on the averaged local diversity the spatial distances between the most diverse and the less diverse provinces were more regular (Fig. 7.4d); the differences described previously between regional and local diversity were only partially explained by this multivariate analysis.

Geographical distribution of diversity properties

The geographical distributions of diversity properties (values per *sq_5x5*) clearly showed the spatial relationship between stomiid diversity and the system of Longhurst (1998b) (Fig. 7.5). The observed contrasts between the three NATR regions (i.e. NATR, NATR E and NATR W) were clear in most of the maps. The figures clearly illustrate the higher stomiid diversity at WTRA, CARB, NATR E and NAST W and the lower diversity at the central NATR, MEDI and northern most provinces. GFST appeared as a marginal continuation of NAST W indicating the relationships between those two faunas. The difference between southern and northern NAST E was also evident from the pictures. North Atlantic endemic species were mainly distributed across the subtropical belt extending their range southward into NATR W, CARB and NATR E.

Taxonomic geographical distribution

The distribution of North Atlantic Stomiidae stomiid species across three latitudinal transects (eastern, western and polar) is summarised in Fig. 7.6. The eastern North Atlantic was dominated by the less derived stomiid sub-families, namely Astronesthinae, Chauliodontinae and Stomiinae and the first sister genera of Melanostomiinae (to *Flagellostomias*). Derived melanostomiids (from *Photonectes* to *Eustomias*) radiated mainly in the western North Atlantic sector, and this was more emphasised for several sub-genera of *Eustomias*. The northern polar provinces were linked with taxonomic branches that extend from both eastern and western provinces. NATR also had affinities with the eastern and western Atlantic as most species in that central province were recorded near its boundaries. Malacosteinae radiated throughout the North Atlantic


a)
S = species
75
65
55
45
35
25
15
5
1
b)
H' = diversity
2.8
2.4
2
1.6
1.2
0.8
0.4
0
c)
J' = evenness
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
d)
Ninf = Hill's number
7
6
5
4
3
2
1
-100
-80
-60
-40
-20
0
20
40
0
20
40
60

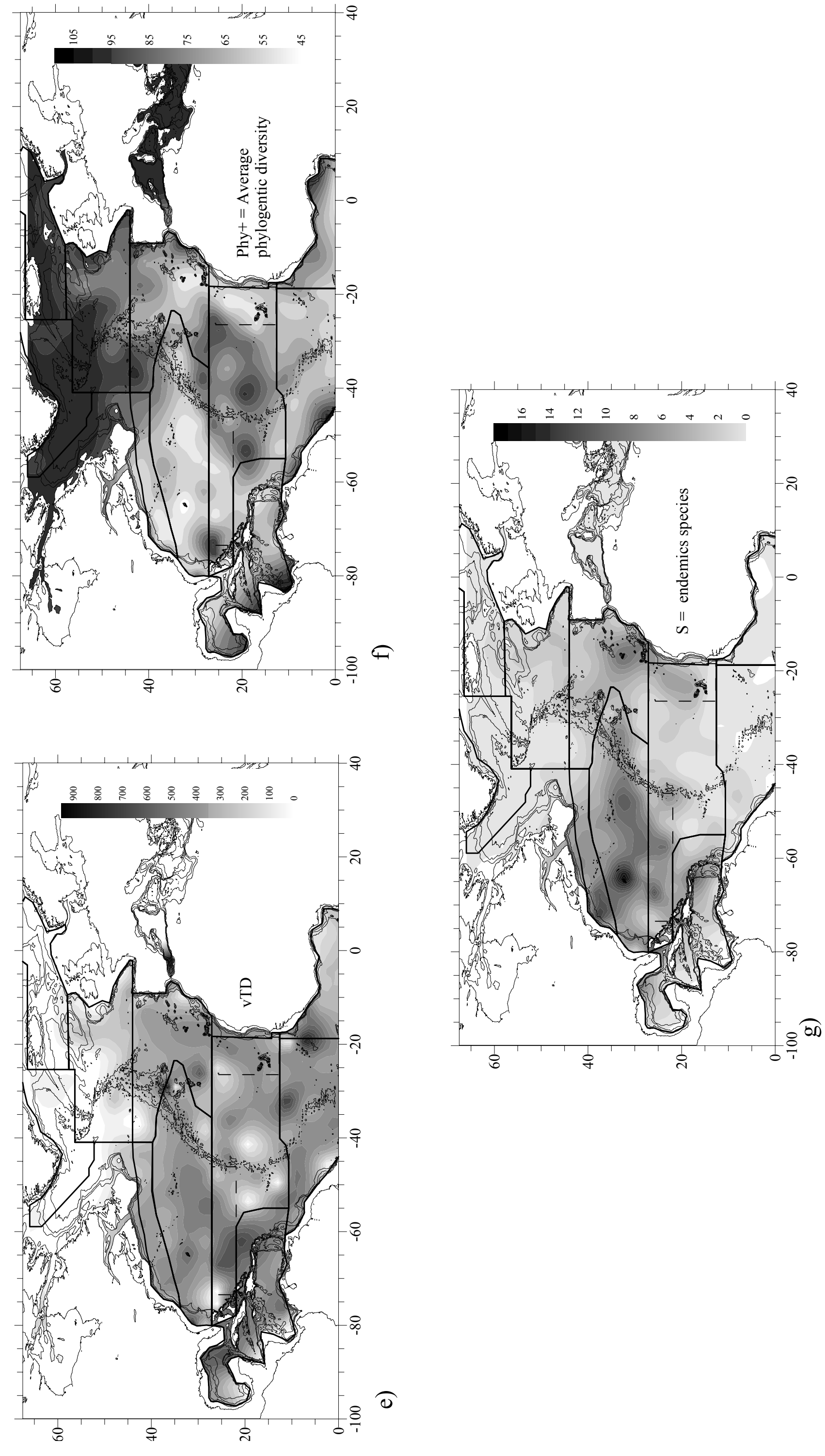


Figure 7.5 Geographical distribution of local diversity of North Atlantic stomiid fish. a) number of species observed (S) ; b) Shannon-Wiener diversity index (H'); c) Pielou's evenness index (J'); d) Hill's number $N\infty$; e) variation in taxonomic distinctness (Λ^+; vTD); f) average phylogenetic diversity (Φ^+); and g) number of North Atlantic endemic species. Gridding (kriging) of values computed for 5° x 5° latitude/longitude squares (*sq_5x5*).

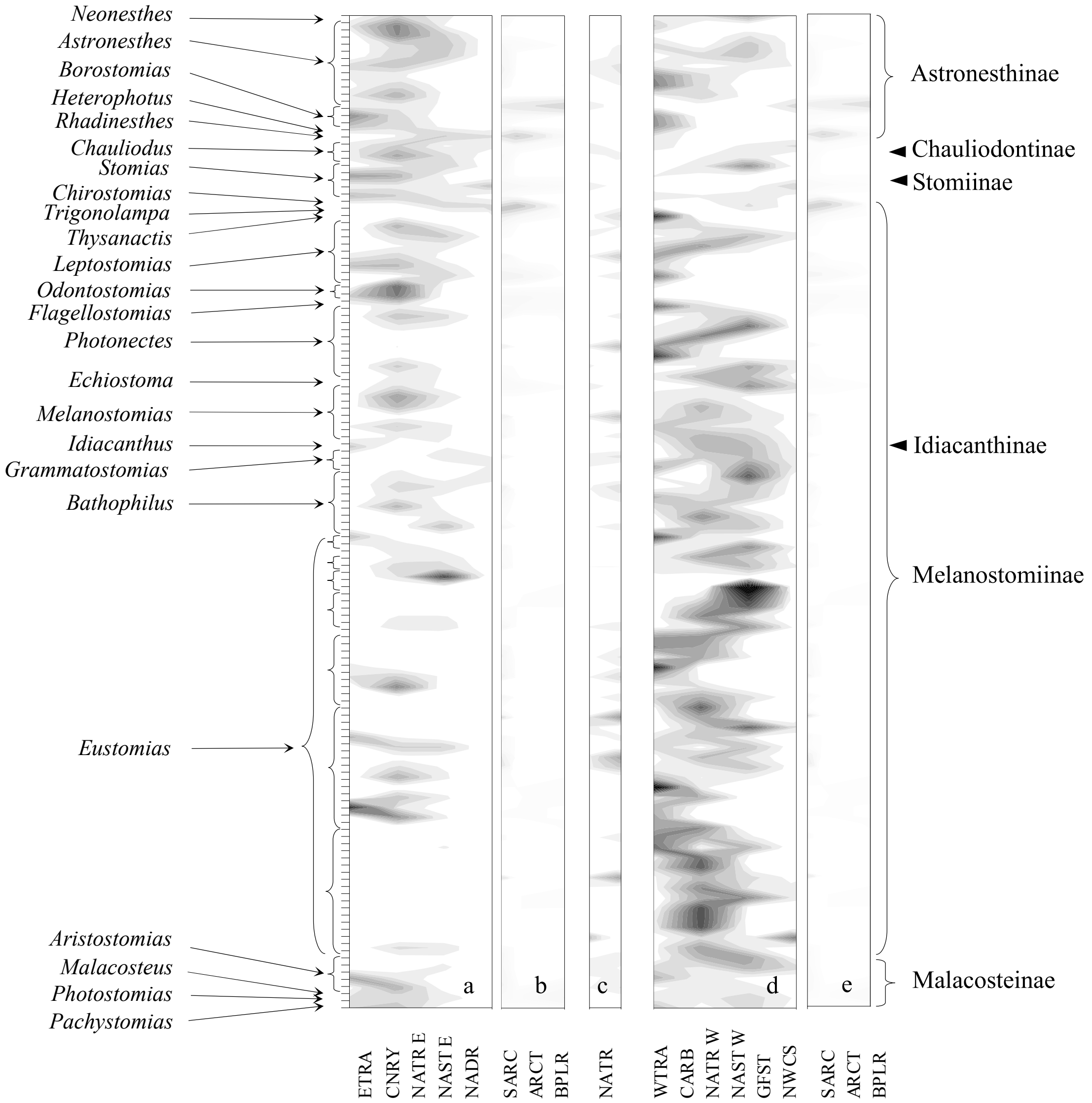


Figure 7.6 Taxonomic distribution of stomiid species (gridding) across latitudinal transects in the eastern, western and polar North Atlantic Longhurst provinces (see Fig. 2.2 for acronyms). The species are organised systematically following the Chapter 5. a) Eastern North Atlantic transect; d) Western North Atlantic transect; b) and e) Polar Biome provinces. NATR is detached from both transects (c).

The North Atlantic Stomiidae assemblages

The composition of the stomiid assemblages varies markedly over the North Atlantic provinces (see SIMPER analysis tables in Appendix G). *Chauliodus* and *Stomias* dominated in most provinces and were the characteristic genera across the North Atlantic.

The stomiid community in the eastern equatorial province (ETRA) was dominated by *Stomias* (*S. affinis*; *S. lampropeltis*; *S. b. boa*), *Chauliodus* (*C. schmidti*; *C. sloani*), some astronesthids (*Borostomias elucens*; *Astronesthes* spp.) and malacosteids (*Photostomias* cf. *guernei*; *Aristostomias xenostoma*; *Malacosteus niger*). The losejaw *P.* cf. *guernei* and *S. affinis* were the most typical. The eastern Atlantic endemic *Odontostomias micropogon* was the central melanostomiid, but the fauna includes few *Eustomias* species, of which two are endemic. Eastern Tropical Atlantic endemics and Amphi-Atlantic distant neritic species were key components of ETRA fauna.

The WTRA stomiid assemblage was more diverse than its eastern counterpart. The less derived stomiids (Astronesthinae, Chauliodontinae and Stomiinae) and some malacosteids also dominated the assemblage but overall the contribution of melanostomiids was much higher. The community included 18 top ranking stomiids. Five (i.e. *C. sloani*, *Astronesthes richardsoni*, *S. affinis*, *Thysanactis dentex* and *Heterophotus ophistoma*) contributed half of the catches. The malacosteids (*A. xenostoma*; *M. niger* and *P.* cf. *guernei*) were also key components of this fauna.

The Canary province stomiid assemblage was clearly dominated by the *Chauliodus* (*C. schmidti*, *C. sloani*, *C. danae*) and *Stomias* (*S. b. boa*; *S. lampropeltis*; *S. affinis*) species. The malacosteids, (*P.* cf. *guernei* and *M. niger*) and one melanostomiid (*Flagellostomias boureei*) were also relatively common in the region. The stomiid fauna of this coastal province was clearly less diverse than that found at the adjacent Eastern Tropical Atlantic. The NATR E fauna was typified by 23 species with diverse biogeographic affinities. The *Astronesthes* genus was represented by six species and contributed greatly to shape that community, whereas the contributions of *Stomias* and *Chauliodus* (with three species each) were less important than in the equatorial provinces. *Eustomias obscurus*, *Melanostomias bartonbeani* and *F. boureei,* among other melanostomiids, were very common in the samples taken at NATR E. Again the malacosteids that have been reported for equatorial provinces were key species in this environment.

The light and slender *C. danae* and *Idiacanthus fasciola* dominated the stomiid fauna in central NATR. The assemblage included other species that were abundant in the adjacent equatorial (e.g. *C. sloani*), eastern (e.g. *P.* cf. *guernei; E. obscurus*) and western (e.g. *Bathophilus pawneei*; *Astronesthes similis*) provinces The western sector of the tropical Atlantic belt (NATR W) was also dominated by *C. danae*, *I. fasciola*, *P.*

guernei, *E. obscurus* but the assemblage included new elements such as *Stomias brevibarbatus*, *Eustomias binghami*, *Echiostoma barbatum*, *Photonectes braueri*, *Eustomias bimargaritatus* and *Aristostomias lunifer*.

Adjacent to both NATR provinces, the Caribbean/Gulf of Mexico region was numerically dominated by the viperfish (*C. sloani*). Then 19 top ranking species of all sub-families graded in terms of importance. Individually, *Astronesthes macropogon*, *S. affinis and Photostomias* contributed 20% to the assemblage. *B. pawneei*, *Echiostoma barbatum* and *Eustomias brevibarbatus* were the most typical melanostomiids.

The ubiquitous species of the subtropical belt include the species that dominate in different combinations in other provinces (i.e. *C. danae*; *C. sloani*; *I. fasciola*; and *P. cf. guernei*). The subtropical *Bathophilus vaillanti* was fairly abundant and appeared for the first time at these latitudes. Other subtropical (and subtropical complex) species contributed notably to the general pattern of the assemblage (e.g. *S. brevibarbatus*; *M. bartonbeani*; *Chirostomias pliopterus*; *Photonectes margarita*; *Photonectes parvimanus*; *Astronesthes gemmifer*; *Photonectes dinema*, *Astronesthes leucopogon* and *F. boureei*).

The stomiid community at NAST E was less diverse with only 10 species typifying its assemblage. In NAST E although the contribution the by the boreal species *Stomias boa ferox* was greater than in the NAST W, the characteristic species of both assemblages were the same.

The stomiid fauna of the Slope Water off Canada (GFST) was marked by the dominance of the widespread *C. sloani* and the boreal *S. b. ferox* combined with a mixture of faunistic elements from the western tropical and subtropical provinces. Toward the north the stomiid assemblages were much less diverse with *S. b. ferox* being the core species. In NWCS the subtropical/ boreal malacosteid *Aristostomias tittmanni* seemed to be a typical species. At those latitudes the cold water stomiid *Borostomias antarcticus* was already an important species. To the west toward the North Atlantic Drift Province the stomiid community was dominated by *S. b. ferox* and *C. sloani*. *B. antarcticus* and the melanostomiids *M. bartonbeani* and *Trigonolampa miriceps* were also characteristic in the eastern boreal assemblage. The other stomiids present were rarely sampled (e.g. *Astroneshes gemmifer*, *F. boureei*, *Grammatostomias flagellibarba*, *C. pliopterus*, *M. niger, A. tittmanni*).

The stomiid assemblages in the polar seas were composed almost exclusively of *S. b. ferox*, *C. sloani*, *B. antarcticus* and *M. niger*; but occasional elements of the southern regions are able to survive under those extreme conditions. The peculiar stomiid fauna of the Mediterranean Sea included the widespread species *C. sloani*, a relict population of the polar *B. antarcticus*, the core population of of the southern form of *S. boa* and the melanostomiid *Bathophilus nigerrimus*.

The same stomiid species were dominant in many North Atlantic provinces the same. The distinctiveness of the assemblages that typify those provinces is based on the relative proportion of these characteristic species together with others that are regionally abundant.

Discussion

The main question when one approaches biodiversity issues is how the observed figures depend of the size and quality of the data available. In other words, how much of the actual biodiversity is revealed by the data. Certainly, most of the techniques to measure biodiversity are dependent of the observed number of species (S) and consequently of the sampling effort (especially in regions not extensively sampled).

The sampling effort computed was unevenly distributed (Fig. 4.3). Several provinces were under-sampled (e.g. ETRA, NATR, CNRY) and there more species are expected to be found as sampling effort increases. Nevertheless, the relationship between sampling effort and number of species showed no clear relationship (Fig. 7.1). Moreover, the different methods such as rarefaction, relative abundance plots, univariate and multivariate analysis of biodiversity indices, showed consistently similar results. Even if biodiversity in some biogeographic provinces will appear different in future approaches, the large-scale patterns of North Atlantic stomiid biodiversity revealed seem unlikely to change much.

The results obtained for ETRA have the highest level of uncertainty. Apart from the low sampling effort undertaken there, only its northern sector has been studied. Some stomiids not reported in this study are known to occur in the southern sector of ETRA. However, in most of the analyses this region was closely related to its adjacent provinces, CNRY and WTRA.

Backus et al. (1977) used the oxygen minimum layer, characteristic of the eastern tropical Atlantic, to delimit the Guinean province. However, no detailed information about species diversity in the province was given because ETRA was clearly under-sampled by the Atlantic Zoogeography program (see maps in Nafpaktitis et al., 1977). Voss (1967) only briefly reported on the results of a pelagic program carried out in the Gulf of Guinea in 1964-65 (data included in *S_db*). The author mentioned a richer midwater faunal assemblage both in terms of species and numbers, compared to other regions, where large fish accounted for about ten times more biomass than that obtained from hauls made at the western Atlantic, using the same sampling protocol. Those observations have not been completely corroborated by the results found for the ETRA Stomiidae assemblage, which showed intermediate species richness and high levels of equitability.

The endemic species along the equatorial and tropical eastern Atlantic can be expected to have life cycles strategies (namely their vertical behaviour) that are tightly adjusted to the complex equatorial currents, otherwise they will disperse into the adjacent oceanic regions (Brunn, 1958). To be ecologically dependent on the continental slopes (i.e. have a benthopelagic life during the adulthood; Parin and Golovan, 1976; Golovan, 1978; Parin et al., 1978) will guarantee the permanence of local populations and the chance of speciation. But even in this case, the pelagic phase of those species needs to be tuned to local circulation (Badcock, 1981; Merrett, 1986; Angel, 1993). The distant neritic species are important components of the ETRA stomiid fauna.

This province is marked by seasonal fluctuations in oceanography and in the moderately high production cycle (Longhurst, 1998b). The relatively low species richness and the high evenness of the ETRA stomiid assemblage (which is dominated by less derived stomiids; Fig. 7.6) may indicate the instability of a system resilient to invasion by new species (especially the more derived melanostomiids). The absence of many western equatorial species in the region may be constrained by abiotic factors (e.g. the low levels of dissolved oxygen) or by biotic interactions such as competitive exclusion driven by the pre-occupation of the available niches. The existence of an important Eastern Tropical/Equatorial endemic fish fauna combined with the absence of many widespread species have also been reported for the Eastern Tropical Pacific (Ebeling and Weed, 1963; Johnson, 1974; Parin, 1984), a region oceanographically comparable to ETRA.

The Stomiidae species that colonised the North Atlantic from elsewhere, needed to cross the equatorial provinces and WTRA is actually the main gateway to the basin (stomiid faunas from both sides of the Panama isthmus are very different). The seasonal (physical and biological) cycles in that province are more stable, and the (primary) productivity significantly lower than at ETRA (Longhurst, 1998b). Stomiidae specific richness and evenness were found to be high, and WTRA ranked among the most diverse provinces, comparable to CARB, NATR E and NAST W. Higher local diversity was found in the WTRA/CARB and WTRA/NATR E boundary regions (Fig. 7.5), where many western equatorial faunal components had their centres of distribution and species that live preferentially to the north had spread to. Weather or not there is faunal input from the southern hemisphere is unknown, but many species are reported either to maintain disjunct equatorial populations or to be endemic to the equatorial waters (see Chapter 6). Some species (e.g. the nyctoneustonic *A. niger*) tend to occur along the crest of the divergent thermal ridge between the North Equatorial Countercurrent and the North Equatorial Current, probably profiting from the enhanced surface productivity along that frontal zone (Yentsch, 1990; Longhurst, 1998b; Stramma et al., 2003). Species from WTRA enter the southern NATR, especially via boundary currents, but also across the frontal ridge, and these expatriates contribute for the overall regional diversity of that province.

The water column in the Caribbean province (CARB) in the Trade Wind Biome is generally permanently stratified and the seasonal productivity cycle is relatively stable (Longhurst, 1998b). High levels of pelagic diversity are expected in a region with intermediate levels of productivity and disturbance as predicted by Huston (1979) and confirmed empirically by Agard et al. (1996) for the Caribbean phytoplankton. In fact, the province was found to hold a diverse stomiid assemblage that is evenly structured (except in terms of biomass). However, CARB is not a “homogeneous” province, as recognised by Longhurst (1998b) and other authors. For example, Backus et al. (1977) defined three provinces and one faunal region within the integrated Longhurst’s CARB (Lesser Antillean, Caribbean Sea and Strait of Florida and the Gulf of Mexico, respectively).

The analysis applied to the CARB pooled data certainly biases the picture of the actual distribution of stomiid diversity in that western tropical region. A detailed insight at smaller-scales is required to characterise the variability, but this was not attempted here. However, based on the geographical distribution of biodiversity properties (Fig. 7.5) and distribution maps of individual species (Appendix G) CARB can be split empirically at least into three faunistic regions (following Backus et al., 1977): 1) Lesser Antilles and Caribbean Sea, which receive equatorial (WTRA) influences; 2) central Antillean islands arc, a centre of origin (speciation) of Stomiidae (especially *Eustomias*) species; and 3) Gulf of Mexico, a terminal body of water mass inhabited by species of several biogeographic origins.

These sub-CARB faunal assemblages are associated with different oceanographic conditions. South Atlantic oceanic water enters the southern regions of the province entrained in giant eddies that throughout most of the year detach from the retroflection of the North Brazil Current (Johns et al., 1990, 1998; Bourles et al., 1999). Many western equatorial species have been recorded there. At the eastern boundary the North Equatorial Current, which flows through the central water mass at NATR, enters the basin through the island passages. Semi permanent gyres are formed by the interaction of the current with the local topography (Schott and Molinari 1996), and these may favour the speciation (mainly of *Eustomias*) associated with the distant-neritic environment. Species with wide oceanic distributions but absent from the inner CARB impinged the Caribbean island arc. CARB (as NATR E) is a biogeographic corridor for species that are absent from central NATR but occur at subtropical and equatorial belts. Hydrographic and seasonal dynamics in the Gulf of Mexico differ from those in the southern Caribbean Sea (Longhurst, 1998b). The stomiid fauna of the Gulf of Mexico includes many species that occur mainly at the western equatorial and southern tropical regions and others that clearly have subtropical affinities, and which were absent from the lower latitudes.

Sutton and Hopkins (1996a) described the Stomiidae assemblage of the Gulf of Mexico and found that stomiids were the most species rich fish family in the region (83 species). Based on the available data, the Gulf of Mexico stomiid fauna was reported to be more diverse than elsewhere. However, in this study the species reported in WTRA and GFST equals that number, and the species richness found at NAST W was clearly higher. Only a small fraction of the large data set compiled by Sutton and Hopkins (1996a) was included in this study. Nevertheless, the six most abundant species found by these authors in the Gulf of Mexico also ranked among the more abundant in CARB stomiid assemblage. A direct comparison between the two studies can not be made as Sutton and Hopkins (1996a) studied only the Gulf of Mexico fauna.

On the opposite side of the North Atlantic lies NATR E, a biogeographic region split from the central NATR (Chapter 6). Even thought this province was under sampled compared with several other provinces (Fig. 7.1) its highly diverse Stomiidae fauna was apparent. The regional oceanography is dominated by the Canary Current, the offshore extension of the upwelling conditions off Mauritania (CNRY) and by the Cape-Verde frontal zone, which oscillates seasonally between 12º to 20ºN. Brunn (1958) was among the first authors to detect the faunal peculiarities of the Eastern Tropical (equatorial) Atlantic. He postulated similarities between the eastern tropical regions of Atlantic and Pacific, but it was Backus et al. (1977), Badcock (1981), Hulley (1981), John and Zelck (1998), among others, who studied the midwater fish fauna (mostly Myctophidae) of the "Mauritanian Upwelling Region". The region was classified by those authors as being myctophid dominated, with northern (boreal) faunal elements than extend their range into the pseudoceanic environment offshore northwestern Africa. Southern NATR E was recognised as an "oceanic hole" because larvae of many oceanic mesopelagic species were absent (John, 1986; John and Zelck, 1998). Few or no endemics (of Myctophidae) were reported for the area (Hulley, 1981).

In this study the Stomiidae assemblage found in the region was highly diverse, structured on species with diverse biogeographic affinities: 1) broadly tropical and widely central species, which accounted amongst the most abundant species; 2) widespread species, with low densities at NATR and spread through this boundary zone connecting northern and southern demographic units; 3) mosaic species that occur mainly at the subtropical belt and/or boreal provinces and maintain isolated "metapopulations" at NATR E; 4) species that live in the subtropical belt and/or boreal provinces and extend their distribution ranges well into the area; 5) species centred at the equatorial waters (WTRA) that disperse northward, often reaching the Canaries islands; 6) amphi-Atlantic distant-neritic species that occur in both sides of the Atlantic; 7) *Stomias b. boa* that spreads from the Mediterranean throughout NATR E and CNRY; 8) eastern tropical distant neritic endemics species that spread from NATR E and CNRY to the southern boundary of ETRA; 9) and finally a few eastern tropical endemic species (*Eustomias*; low range) that live around the Cape-Verde Archipelago waters.

The observations showed that in NATR E stomiid species richness is the highest in eastern Atlantic matching the latitudinal profile presented by Badcock and Merrett (1976) and Angel (1993, 1997). This boundary zone shows high species richness resulting from the mixing of faunas as noted Pierrot-Bults (1997) and observed by Reid et al. (1978) in the Pacific Ocean.

Probably, only some of the stomiid groups (biogeographic and taxonomic) are able to sustain viable populations within the province (i.e. complete their life cycles) and thus contribute to future biodiversity (van der Spoel, 1994a). The upwelling regions were recognised as important centres of pelagic speciation (points of stress of Angel, 1997) and van der Spoel and Heyman (1983) considered explicitly the Mauritanian (Dakar) upwelling centre as important on a global context. As for the ETRA, the species that live in NATR E also need to have life history strategies to cope with the mesoscale circulation and production cycles. Apart from the narrow relationship that many of the distant-neritic eastern tropical fish species maintain with the benthopelagic domain (e.g. Parin and Golovan, 1976; Golovan, 1978; Beklemishev et al., 1977; Parin, 1984) nothing is known about that predicted bio-physical coupling.

In terms of species diversity the coastal CNRY province is the landward extension of NATR E. The faunistic similarities of both regions (and ETRA) are evident. However, the CNRY stomiid assemblage has considerably lower species richness, as could be expected for a neritic/ coastal region.

The NATR province is the homogeneous tropical central water mass, characterised by the flow of the North Equatorial Current, which is the southern limb of the North Atlantic anticyclonic gyre. This highly oligotrophic region (the big blue hole) has attracted little interest from the international oceanographic community (Longhurst, 1998b), a fact reflected also by the small amounts of material available from this vast region. Nevertheless, the large-scale pattern of NATR stomiid diversity distribution seemed clear. The relatively high diversity computed from regional (provincial) data was biased by the faunistic influxes from the adjacent species-rich provinces (WTRA, CARB, NATR E and W and NAST). When local data were considered the central waters of NATR were shown to be impoverished of stomiid fauna.

Classical theory implies that the (almost) permanently stratified central tropical waters are mature and stable reservoirs of species diversity (both in numbers and phylogenetically) (e.g. Ebeling, 1963; Johnson, 1982; McGowan. and Walker, 1985; McGowan, 1986; Angel, 1997; Johnson and Zahuranec, 1998). The predictable gyres are thought to have a high niche dimensions and complex trophic interactions structured by small organisms on low productivity (e.g. Angel, 1997). Clearly this was not the picture depicted for Stomiidae as the central waters of NATR were dominated only by a few slender body stomiid species (e.g. *C. danae*, *I. fasciola* and *P. guernei*). It seemed then that the low productivity (Longhurst 1998b) associated with high stable systems tends not to create biotopes suitable for most of these top mesopelagic predators stomiid fishes.

NATR W was identifiable (Chapter 6) based on the disparate figures on stomiids distribution and diversity between the region and the central NATR (e.g. Fig. 7.5). This area roughly coincides with the South Sargasso Sea of Backus et al. (1970, 1977) and includes the tropical limb of the "eye" of the anticyclonic gyre as well as the Antilles cell along its western boundary (Fig. 6.3; Schott and Molinari, 1996). This circular mesoscale feature may be important in the retention of species that maintain viable demographic structures in the province. NATR W was moderately well sampled and Stomiidae diversity was thought to have been relatively well identified. Species richness is clearly higher than at NATR, but lower than in the adjacent NAST W and CARB. The relatively high stomiid species richness of this province was not expected from extrapolating the similarity of the regional oceanography between NATR W and central NATR as defined by Longhurst (1998b) (also from Backus et al. [1970] figures). Several species appear to have their northern or southern limits of distribution along the weak thermal front that lies across NATR W and NAST W boundary, as referred for myctophids by Hulley and Krefft (1985). Nevertheless, the boundary is relatively permeable and the diversity of NATR W included several subtropical species (from NAST W) that were able to cross it and survive into NATR W. Those species combined with the faunistic inputs from CARB, definitely contributed to the overall species richness observed in the region. Several species were considered to be endemics in NATR W.

The Northern Sargasso Sea (especially around Bermuda Islands) is the best-studied province (along with GFST). The region is entirely dominated by the 18ºC Mode Water of the western subtropical gyre (Worthington, 1986), delimited to the west and to the north by the Gulf Stream and to the east by the Azores Current. NAST W experiences a moderate range of seasonal variability (disturbance) of the water column stratification and of the production cycle (Longhurst 1998b). The province proved to be among the most diverse with the highest species richness, moderate levels of dominance and high percentage of rare species. Various (western and wide) subtropical endemics species were reported for the province (especially species of *Eustomias* but also *Astronesthes, Chirostomias, Photonectes* and *Bathophilus*). Non-endemic subtropical species, many of them showing a bi-subtropical pattern of distribution in the Atlantic, were important components of the fauna. The tropical jet current that leaves the Caribbean Sea and the Gulf of Mexico as the Gulf Stream carries tropical expatriates toward the northern latitudes. Cold core (Slope Water) rings, advected throughout the province, generate local disturbances and meso-scale pockets of enhanced productivity (Ring Group, 1981; William and Follows, 1998) and carry with them expatriated boreal species that contributed moderately to local and regional diversity (Jahn, 1976; Backus and Craddock, 1982). This faunistic component includes for example *Stomias boa ferox* and the northern form of *Astronesthes niger*.

The western sector of the subtropical province (NAST W) is the region that contains the most typical pelagic stomiid assemblage in the North Atlantic. Again a moderate seasonally disturbed environment of the western half of the basin supports high levels of biodiversity.

The GFST is one of the best studied provinces. Amongst the many cruises that targeted the midwater fauna of the region, the extensive program developed by the DFO and University of Dalhousie University deserved reference, as it covered the seasonal cycle over several years (Themelis, 1996). The Slope Water is the example of a region that holds high species richness, mainly because of expatriation. It has been postulated that meso-scale warm core rings and extrusions of subtropical water are responsible for dispersing the diverse Northern Sargasso pelagic fauna into the province (Craddock et al., 1992; Themelis, 1996, among others). However, species from tropical provinces (namely CARB) that were absent from NAST W were also reported to occur in the area; it was suggested (in Chapter 6) that the Gulf Stream advects species directly from CARB that can survive temporarily into the western and warmer Slope Water.

The region is characterised by strong variability of the seasonal cycle (Longhurst, 1998b), reflecting the extension of polar waters inputs from the north by the Labrador Current and the intrusions of northern Sargasso Sea water into the basin from the south. McKelvie (1985a, b) reported an ecotonal faunistic gradient along a north-south transect, within the province. Themelis (1996) rejected this ecotone classification for the region although she found a similar gradient. On average the warmer southwestern GFST fauna has higher diversity and equitability relative to the colder Newfoundland waters. Seasonal changes in diversity were reported by Themelis (1996) who found an increase in species richness from winter-spring to summer-autumn, which was explained as reflecting the life-cycles of short lived species advected from the Sargasso Sea. The effect of seasonality on the composition of GFST stomiids were not studied here, but it seems probable that the drop of temperature (and disturbance) during the winter will reduce the survival of sub-tropical and tropical species, even if they are being continuously advected in by Gulf Stream and the warm core rings. Also some sub-genera of the tropical *Eustomias* genus (e.g. *Biradiostomias*, *Dinematochirus*) that occur in NAST W and were absent from the province may not be able to survive in the region. The relative abundance of southern elements in GFST is much lower than in NAST W but the percentage of occurrence of rare species was at its maximum; dominance is clearly higher than in the subtropical belt and the sizes of GFST specimens were generally larger than in NAST W. These observations agree with the patterns reported by Jahn and Backus (1976).

Most of the tropical-subtropical species that seasonally are able to survive within the ecology of GFST do not reproduce there. The Slope Water is probably a sterile expatriation zone for those stomiids as it is for the two subtropical myctophid species studied by O'Day and Nafpaktitis (1967). *C. sloani* and *S. b. ferox* are the only stomiids reported to reproduce in the area (Themelis, 1996), but it is probable that *A. niger*, *M. bartonbeani*, and *Aristostomias tittmanni* also sustain viable demographic units in GFST. *Eustomias quadrifilis* is known only from this region but only the holotype has ever been reported. The province also supports components of the northern polar assemblages; *B. antarcticus* dwells mainly along the slopes that border the province at its northwestern side. Despite the high number of species recorded for the region, GFST harbours a lower stomiid diversity than NAST E.

The northwest-southeast branch of the Azores Current, originates at the bifurcation of the Gulf Stream extension (Fig. 6.3; Klein and Siedler, 1989; Käse and Krauss, 1996) delimits the western border of the eastern subtropical province (NAST E); it then inflects to the east and meanders zonally to the Gibraltar Strait (Siedler and Onken, 1996). NAST E is divided by the Azores Current into southern and northern regions. Many authors considered that the Azores Current corresponds to the subtropical front, and is the northeastern edge of the subtropical gyre (Gould, 1985; Alves and Verdière, 1999, among many others). Just south of the Azores archipelago the current split in two branches, which bound a triangular region centred at Madeira (Klein and Siedler, 1989; Siedler and Onken, 1996; Jonhson and Stevens, 2000). It is here that the “Madeira Mode Water” forms; this is a large, thick, homogeneous sub-surface subtropical water mass that is similar to the 18ºC Mode Water spreads throughout NAST W (Siedler et al., 1987; Siedler and Onken, 1996). To the north and east of the Azores Current, and to about 42ºN (the northern boundary of NAST E), the midwater environment is characterised by the warmer and saltier tongue of water that outflows from the Mediterranean into the Eastern Atlantic (Käse and Zenk, 1996, Iorga and Lozier, 1999a). This roughly corresponds to the northern part of the Mediterranean Outflow province defined by Backus et al. (1977). These oceanographic differences have induced a faunistic sub-partitioning of NAST E that is not depicted in the Longhurst’s system.

Faunistically, the NAST E has ecotonal properties with marked changes across the branches of Azores Current. It is a stomiid impoverished subtropical region (relative to NAST W) where many of the derived stomiids that radiated in the west (e.g. *Bathophilus*, *Eustomias*, *Aristostomias*, among other genera) are scarce. NAST E showed intermediate levels of diversity between NATR E and NAST W and NADR; it is a region with low endemism, thought existent at the southern part.

The Madeira Mode Water (i.e. southeastern NAST E) contains a much higher stomiid diversity than in the northern NAST E. The stomiid fauna of the region is complex and includes species with very different biogeographic origins: 1) tropical and equatorial species that spread across NATR E and find their northern limit of distribution at the Azores Current (see Chapter 6); 2) a number of subtropical species that occur throughout NAST W but are confined to the southern 18ºC waters in NAST E; 3) species with centres of abundance to the north that extend their ranges into the region; and 4) anti-central widespread species that distribute southward along the eastern tropical Atlantic, probably profiting from the upwelling conditions landward of Canaries. Although within the NAST E species richness is clearly higher in the southeastern corner a decreasing gradient in most diversity properties northwestward was apparent. That pattern may be related to expatriation (dispersal) toward the Azores region via the intense eddy field associated with the Azores Current (Stammer and Böning, 1996; Alves and Verdière, 1999) as discussed in Chapter 6.

No faunistic elements specifically associated with the Mediterranean outflow were detected, as reported by Angel (1997). The weak longitudinal discontinuity in diversity properties associated with the NAST E sector of the Mid-Atlantic Ridge (MAR) most probably reflects the topography and the differences in the circulation at both sides of MAR (Bower et al., 2002).

Nevertheless, a more detailed study will be necessary to elucidate the influence of Mediterranean water on the distribution of Stomiidae. Clearly the group is poorly represented in the Mediterranean Sea, by only four species. The MEDI stomiid fauna relates mainly to that of SARC and ARCT and two species that actually dwell in the basin are considered to be relicts from last glacial periods (e.g. *Borostomias antarcticus* and *Stomias boa boa*; see Chapter 6).

The strong faunal discontinuity in the North Atlantic at about 40º - 42ºN was observed long ago and it has been related to the seasonal instability of the system to the north (e.g. Angel, 1979). The boundary has not been associated with any major hydrological feature but to the seasonal cycle of physical and biological properties. The switch of stratification/mixing of the upper layers leads to a pulsed productivity cycle (the spring bloom and the small autumn bloom), a signal that propagates through the entire pelagic food web (see Haedrich, 1986 for myctophids). The boundary in the North Atlantic is more clearly seen between NAST E and NADR. The North Atlantic Drift province is characterised by the southern branch of the North Atlantic Current (Bower et al., 2002) and eastward and south-eastward flow of uneven, random and energetic current bands formed in the westernmost branch of North Atlantic Current (Käse and Krauss, 1996). The seasonal levels of physical disturbance are considered excessive for high levels of species diversity to be maintained, surpassing the limits of tolerance of many tropical and subtropical species. At NADR the species diversity declines sharply as does equitability. The community is composed of a few dominant boreal and widespread species, with important inputs of biomass from the polar provinces, and of species which are otherwise subtropical and tropical. Many of these rare but recurrent expatriates probably play a limited role on the ecology of this ichthyocoenose.

Kukuev et al. (2000) studied the biogeography of this boreal transient zone and derived a similar picture. However, the authors designated several important species (as *C. sloani*, *T. miriceps*, *F. boureei*, *M. bartonbeani* and *M. niger*) as having widely-tropical patterns of distribution; a conclusion not corroborated by this study. Fock et al. (2004) depicted a more complex pattern of NADR midwater fishes assemblages especially associated with the Mid-Atlantic-Ridge. Among the stomiids *C. sloani* and *S. boa ferox* were found to be key species especially associated with the Ridge. As in other regions some stomiid species associated with the continental slopes of the Northeastern Atlantic. However, the number of stomiid species reported to occur in the benthopelagic layers of the NADR sector of the Mid-Atlantic Ridge, seems higher than along the European slopes (Gushchin and Kukuev, 1981; Kukuev, 2004). This deserves further investigation, but maybe such differences are to be expected for a region bordering the western basin where stomiid diversity is in general higher.

The provinces situated to the north of the North Atlantic Current and the associated Subarctic (or Polar) Front have stomiid communities dominated by four species, each one belonging to a different sub-family (*B. antarcticus*, *C. sloani*, *S. b. ferox* and *M. niger*). This taxonomic equitability of polar faunas contributes to the unexpected relatively high values of diversity obtained from some indices. At SARC the influence from the southern provinces is more marked and a few individuals of several species were caught at its southern boundary (e.g. *T. miriceps*, *C. pliopteus*, *L. longibarba, F. boureei*, and *M. bartonbeani*). Further to the north, however, all but one or two species disappear probably restrivted by the extreme conditions of the environment. *M. niger* is considered one of the most specialized fish species that belongs to a clade of highly derived stomiids. Probably this species extended its range into the polar environment much later than *Borostomias*, *Chauliodus* and *Stomias*.

Conclusions

Diversity of North Atlantic Stomiidae is high relative to other pelagic groups. As expected for pelagic organisms local diversity is high throughout most of the area (warmwatersphere), but still low compared to the regional pool of species. Genetic diversity of species that are distributed across several ocean basins can be expected to be higher than first thought, as many disjunct distributional patterns were observed. If the species concept for the group is valid, then the rate of speciation of *Eustomias* is much higher than in the other genera (even among coastal and demersal fishes). However, species that belong to much less derived and less speciose genera (i.e. *Stomias* and *Chauliodus*) dominates the North Atlantic stomiid assemblages.

Stomiidae diversity is highest in the western equatorial waters, along the eastern and western boundary currents and at the western subtropical province. Species and phylogenetic richness peak in the western Atlantic, in the complex CARB province and in NAST W. It declines toward the equator (especially at ETRA), the eastern tropical Atlantic and obviously towards the poles. The highly oligotrophic water mass associated with the North Atlantic Equatorial Current creates a void in Stomiidae species richness and only a few slender stomiid species are abundant in the region. Equitability in numbers decreases from the equator (ETRA and WTRA) to NADR but increases again toward polar waters; it is not linearly correlated with species richness. The number of rare species is higher in the subtropical belt (and particularly in the Slope Water) than in the tropical and equatorial provinces. The North Atlantic stomiid endemic species are more numerous in NAST W, NATR W, NATR E and southern NAST E.

Equitability in biomass diminishes considerably at the tropical boundary currents (distant neritic environments) where species with more k-selected strategies (large bodies and long life-span) while not being numerically dominants, dominate the biomass (conservative species). They are mixed with many other species with r-strategies that are short-lived and small sized and so are dominants in numbers. At the central tropical waters the small body species are dominant both numerically and in biomass. “Older” taxa (namely astronesthids) are apparently absent.

Intermediate levels of seasonal variability (and disturbance) associated with a moderate levels of production seem to be the ideal biotopes for midwater top predators fishes such as the Stomiidae to became highly speciose.

Chapter 8 - Final remarks

This Stomiidae database (*S_db*) is probably the largest set compiled for any group of micronekton organism in the North Atlantic. Just to give a comparative measure of the extent of *S_db*, the following examples are given: Longhurst (1998b) compiled data about the relative composition of zooplankton assemblages in his provinces (standardized first-order; high taxonomic groups) from 4166 stations, from all oceans; the data were archived at several sorting centres (mainly at the Smithsonian Institution); Backus et al. (1977) for the pelagic zoogeography of the Atlantic used Myctophidae collected by 1022 haul-nets made with an Isaacs Kid Midwater Trawl (IKMT 10'), distributed mainly throughout the North Atlantic. The Stomiidae database includes 8185 pelagic net-hauls only from the North Atlantic.

To have material from a range of sampling devices is obviously a disadvantage when direct comparisons between hauls and assemblages are intended. However, one major advantage of assorted data is that it provides a fuller picture of the fauna under study, by sampling the entire size-spectra of their components; each gear offers a representative "window" of a specific size and type of the biota according to its selectivity. The attempt made to standardize the sampling effort produced by the different gears was done to analyse the stomiid distribution data in terms of relative abundances. The problem is complex (and multivariate), because many procedural variables are involved (mainly related to the gear characteristics and the sampling strategy adopted), and because the inherent problems associated with variability of the pelagic fauna distribution at low spatial and temporal scales. Improved statistical methodologies might produce more precise results, but the figures obtained for distributional data, weighted by the computed net-score, do not seem to have diverged to much from reality (i.e. by comparing with species distribution based on absolute numbers only).

The data available comprise a significant proportion of all stomiid collections made throughout 150 years within the North Atlantic. According to the Stommel diagram adapted to space-time variability of biogeographic patterns (Haury & McGowan, 1998), the data has a time scale appropriate to evaluate the biogeographic patterns within the

North Atlantic. The *S_db* contains much more information than was used in the analyses. For some but not all regions it assembled data that enable detailed examination of the assemblage structure, dynamic and distributional patterns at smaller scales; e.g. at regional level or across biogeographic boundaries. In addition, a large set of data on vertical distribution of the stomiid fish is now available, but this was beyond the scope of what could be treated in this thesis. Other relevant information that could not analysed includes: morphological and ecological data for every species in the database; seasonality data, that allows for inferences on variability of species composition across the seasons (at least for some of the better sampled provinces); size and development stages, that may be used to inform about the different ranges of a species (i.e. reproductive and expatriation areas), among many other subjects that are size related.

The initial objective of this study was to relate the distribution of stomiid species and assemblages to a broad range of climatological data that potentially may explain some of the observed patterns. The data source selected was an oceanographic database of the North Atlantic retrieved from the National Oceanic Data Centre (WOD 98'; 1904-1990; Lozier et al., 1995). The development of a Geographic Information System (the most promising analytical tool for large-scale biogeography/ biodiversity studies) was attempted to analyse both biological and climatological databases. However, after preliminary incursions the application of GIS technologies was found to be highly exigent in time, power computation and advanced expertise (especially when applied to a three dimensional dynamic environments, such as the water column). Faced with these constrains, the best option was considered to be detailing the large scale biological patterns contained in the database and creating a solid framework for future research. The data now available are in a format compatible with mathematical models (as in GIS), and ultimately will generate progress. Nevertheless, a well founded background biological rational will be essential to the critical assessment of results obtained by modelling. This is especially true because empirical biogeographic and biodiversity studies on pelagic organisms are scarce and the existing knowledge is meagre.

The Stomiidae have been showed to be a valuable group to study the biogeographic and biodiversity patterns in the North Atlantic. The high numbers of species and their taxonomic diversity enable the detection of different biogeographic/ biodiversity patterns that could be discriminated unless a species rich group had been chosen. Nevertheless only a comparative analysis with other taxa will enable the recurrence of the patterns observed to be evaluated. It would be relevant to assembled basic distributional data with similar levels of accuracy for other pelagic groups.

The eco-biogeographic system of Longhurst (1998b) was expected to provide a functional background to the description of the observed patterns of Stomiidae biogeography/ biodiversity. However, incongruences were apparent between the Longhurst system and the distribution of Stomiidae, especially in NATR, CARB and NAST E (i.e. Chapters 6 and 7). To resolve the problem NATR was split in NATR E, central NATR and NATR W, faunal regions that conform to previously defined systems, viz Backus et al. (1977). Probably the most unexpected result was the absence of many stomid species from the central NATR, a strongly stratified stable oligotrophic region that has been predicted would support high levels of diversity. At the other level, the existence of diverse and complex biogeographic distribution patterns within the basin was clearly revealed. To elucidate several pertinent questions (e.g. the degree of isolation between demographic units of “mosaic” species) future genetics studies are a priority.

This study set out to improve understanding of processes and patterns in the pelagic environment. As emphasised, data mining (on museums repositories and published data) is an indispensable step to achieve that goal. Firstly because the activity will furnished the necessary volume of data needed to study the realm (to sample the realm *de novo* is logistically unrealistic); secondly because only analyses of historical data will enable the detection of responses by biota to decadal scale variability (changes) in climate associated with global changes. The large-scale electronic facilities now available, makes such data mining feasible. Presently, very few exhaustive databases have been compiled containing historical information (not considering fisheries databases). The Stomiidae database will be available to be integrated in several international initiatives such as the OBIS (Ocean Biogeographic Information System**),** the FishBase, and other electronic data centres on biodiversity/ biogeography (e.g. MARBEF, a marine biodiversity European network).

Beside the purely scientific interest of studying the midwater ecosystems, the knowledge gathered can be integrated into dynamic models directed to fisheries assessment and associated with conservation issues (e.g. detect trophic cascades in seamounts resulting from overexploitation; Ecopath type models). Large space-time data series on midwater fauna distribution can also be a useful tool to predict and evaluate the impacts of global shifts in remote ecosystems.

The impact of anthropogenic activities on the structure of the oceanic communities is almost unknown. The use of mesopelagic fauna to evaluate the global impacts of e.g. s dynamics of the spread of pollutants is a new field reqiring future attention.

Krause and Angel (1994) emphasised the intrinsic value of pelagic biogeography/ biodiversity and the weak impact it has on global biodiversity conservation policies. Socio-economic contributions, scientific outputs and contact with the wide public have to be a priority. The authors listed the potential uses of pelagic biogeography/ biodiversity and gave for in evidence areas in which this knowledge is crucial (i.e. palaeoceanography, biogeochemical processes). Networking, monitoring, data integration, modelling and prediction, are key words for future research. A technology-driven science should be improved, but basic information concerning the distribution of biological identities is a fundamental requirement for the progress of the science.

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BIOGEOGRAPHY AND BIODIVERSITY OF STOMIID FISHES IN THE NORTH ATLANTIC

Appendices

Appendix A

The "Ecological Geography of the Sea"

The Longhurst's (1995, 1998ab) Ecological Geography of the Sea system was the biogeographic framework adopted in the present study.

The system represents an important improvement on the ecological perspective of pelagic biogeography. It integrates an ecological component into the regional oceanography. The author suggested that phytoplankton/chlorophyll seasonal dynamic cycles, as perceived by satellite imagery and calibrated by archive data, can be used to draw conclusions about the ecology and diversity of a given biome and province. The geographical variation of the patterns was summarised by a set of measurable oceanographic parameters. The objective was to achieve a level of prediction comparable to that terrestrial ecologists have when they infer about the community by the recognition of a vegetation facies.

Phytoplankton dynamic

The ecological dynamic of the phytoplankton (based on algal physiology) was related with a selected minimal set of factors to predict the first order sequence of the seasonal algal growth cycle (e.g. latitude, seasonal irradiance; photic depth; local wind regime; distant forcing of pycnocline depth; nutrients in intermediate waters). Those factors characterized the regional oceanography. The seasonal topography and stability of the pycnocline have a central influence on algal processes. The phytoplankton dynamic was characterized by a series of integrated parameters from surface chlorophyll fields and chlorophyll vertical profiles (e.g. primary productivity rate and productivity at the deep chlorophyll maximum, DCM). Potential phytoplankton production through the photic zone was computed for the whole ocean.

Satellite imagery (CZCS) provides the biomass index that was evaluated comprehensively at global scale and at all seasons (surface chlorophyll field). The data were validated by archived data (NOAA/NODC), which allowed for the integration of other phytoplankton parameters. Data relevant for the model included global climatology of mixed layer depth, the Brunt-Väisälä frequency index (related with the stability of the pycnocline), the computed photic depth, the surface nutrient field, etc.

The partitioning of the system

The system divides the seas in four biomes and fifty-one provinces, considered as the primary and the secondary hierarchical regions.

Biomes

The biomes were bounded by regional discontinuities in resistance of the pycnocline to vertical mixing (i.e. Brunt-Väisälä buoyancy frequency). The parameter reflects stratification and nutrient supply. Distant and local forcing of local algal dynamics was noted as a key difference between the Trade Wind Biome (TWB) and the Westerly Wind Biome (WWB), respectively. The WWB mix depth layer (MLD) is forced by local winds; seasonal irradiance and winter mixing are important factors. The TWB MLD is forced by geostrophic adjustment to often-distant wind field, and the stratification is strong and quasi-permanent. The partition of the Polar Biome is the result of seasonal ice melting and formation of a brackish surface layer, separated by a sharp vertical density profile from the underlying water masses. The recognition of a homogenous global-wide Coastal Biome was not supported by the data because of the complex physical processes observed along coastlines.

The boundary between the TWB and WWB is about the equatorward limb of the subtropical-tropical gyres that in the North Atlantic is the northern flank of the NECC, at about 20ºN. The boundary follows the edge of the tropical surface waters more closely than the frontal system. The WWB extends poleward to the Polar Front, which is the boundary of the Polar Biome. The coastal regions are defined by the seaward extent of the coastal physical processes.

It is argued that discontinuities between the biomes should be verified by a wider set of ecological characteristics (e.g. changes in food-webs, seasonal cycles of zooplankton, or taxonomic turnovers), but no consistent information is available to make such comparative analysis. Nevertheless, the author attempted to test the validity of his partitioning using distributional data of epipelagic biota, clustered into high taxonomic levels (e.g. Phylum or Class) and trophic groups. The results were indicative but quite diffuse.

Provinces and boundaries

A province was viewed as a region that responds in a unique way to seasonal and spatial patterns of primary production of algae (as the Biogeochemical Provinces of Platt & Sathyendranath, 1988). The partitioning of the sea into provinces integrated factors related to regional oceanography (resistance of MDL; regional bathymetry; surface circulation; presence of geographic features [i.e. islands, seamounts, ridges]; and distribution of landmasses) and the shape of the chlorophyll profiles and other photosynthetic parameters.

An a priori assumption was that the entire ocean should have about 50 compartments convenient for computation of primary production. The analysis developed by detecting repetitive regional patterns of surface chlorophyll enhancement (by analysis of CZCS imagery) was used as a proxy for the local phytoplankton dynamic. Surface discontinuities also detected by remote sensing, supported the preliminary identification of boundaries. Then the mixed layer topography, the seasonal wind stress, wind stress curl, heat fluxes, distribution of oceanic frontal zones and studies on regional plankton ecology (e.g. growth, consumption or sinking rates) were used to analyse each of the divisions.

Finally, the distribution of archived data (containing parameters that represent the attributes of a province) in each compartment (province) and season, was compared statistically between pairs of adjacent provinces. The partitioning was accepted because a change through a boundary induces a predictable response in the phytoplankton dynamic. The deep chlorophyll maximum (an integral of nutrients, light and density) was found to be the most consistent feature of chlorophyll profiles and was selected as a good criterion for testing the province boundaries.

The somewhat free position of the boundaries between the biomes and between provinces reflects the temporal and spatial variability of the pelagos. The boundaries are recognised to be blurred rather than precise. They are approximately time-averaged and the final selection of coordinates for the boundaries can be made sensitive to the data field.

At the boundaries turnovers in pelagic distributional patterns, food-webs and general complexity of the ecosystems are expected. At a less reliable degree of confidence, Longhurst discussed the zooplankton dynamic (e.g. vertical and ontogenetic migrations patterns), the expected complexity of food-chains, the biodiversity, and other important ecological properties, that eventually distinguish each compartment. The spatial coverage of the North Atlantic biomes and provinces are presented in Chapter 2 (Fig. 2.2).

The system and the classical pelagic biogeography studies

The Ecological Geography of the Seas is a technology-driven approach to pelagic biogeography. The author illustrated it by contrasting the method developed to those used by the classical perspective of the science, based on distribution of taxa. The criticism to conventional methodologies (or their absence) used by pelagic biogeographers seems fair and competent. However, despite the lack of ability to capture data (at high fluxes), the "fill-in" taxonomic biogeography ("an intractable scientific problem"), appears vital to support (or not) the Longhurst's biogeographic scheme. If ecological distribution patterns of organisms (e.g. population and communities) coincide with the biogeography provided, the potential of the systems for global application will increase. No especial attention was paid to the evolutionary history of the pelagic realm or even to the responses to temporal (decade to centuries) variability, because the inaccuracy and paucity of available data.

Appendix B

Ichthyological collections of North Atlantic midwater fishes - an inventory using the Stomiidae fish family as a proxy

Introduction

Natural history museums and other biological collections constitute the major repositories of known global biodiversity. They hold the reference type material, the standards of species diversity, and maintain valuable material and data to reconstruct the biological communities that lived in a given place at a given time, even before the era of the greatest anthropogenic impacts on the global ecosystems.

For many decades voucher specimens have been used primarily by taxonomists. However, the natural history collections certainly provide relevant data for studies on evolutionary biology, biodiversity, biogeography, ecology, conservation, ecotoxicology, fisheries biology, etc. Biological collections also play a key role in educational programs and public outreach activities by supporting exhibitions, publications, and multimedia outputs for large audiences.

Biodiversity and biogeographic have stimulated the networking of electronic biological data sets available in natural history collections world-wide (Pierrot-Bults, 1998; Grassle, 2000; Paterson et al., 2000). However, the potential of those e-resources to describe past and present distribution patterns of organisms is presently underused. To assess exhaustively the existing samples of a species, or of a group of species, is still today an extremely demanding task, and was virtually impossible prior to the Internet age.

Many ichthyological collections, mainly American, have on-line electronic catalogues, but a considerable amount of data, mainly in European institutions, is accessible only from the traditional card file catalogues. Unfortunately, various large ichthyological collections, mainly from the eastern European countries, remain uncatalogued. Optimistically, some international electronic initiatives may encourage the recovery of some collections, the general implementation of on-line e-catalogues, and the networking of those biodiversity centres. Indeed, several ichthyological collections are already contributors for international on-line initiatives such as the FishBase (Froeser and Pauly, 2000; www.fishbase.org), the FISHNET (http://habanero.nhm.ku.edu/fishnet/), the FishGopher project http://www.as.ua.edu/biology/uaic/fishgopher.html. FishBase and FISHNET are data contributors to OBIS (Grassle, 2000; http://www.iobis.org) and other Census of Marine Life (CoML) electronic projects (Vieglais et al., 2000).

Collette and Lacnher (1976) and Poss and Collette (1995) compiled metadata about North American ichthyological collections, and Kottelat et al. (1993) inventoried the European counterparts. The collections were identified, and their holdings (i.e. numbers of specimens, lots and type material) summarised. The studies also mention the habitats sampled, the geographical areas covered, and reference the existing type catalogues, etc. The American institutions were compared, ranked, and indexed according to their holdings, growth rates, technical activity, etc. These contributions are extremely valuable, but they are necessarily general and the actual content of each ichthyological collection was only briefly covered.

This survey compiles metadata about the collections of North Atlantic midwater fishes. The collections were characterised by their Stomiidae holdings (a diverse family of midwater fishes; see below), which were used as a surrogate for the holdings of all the midwater fish fauna in general.

Material and methods

Data source

The information for this survey was retrieved from a database that primarily assembled occurrences of North Atlantic stomiid fishes. The Stomiidae database (*S_db*) contains taxonomic, geographical, biological, and cruise data. The stomiid holdings of fully computerised e-catalogues were either downloaded from the collection web site or received from the institution. Other collections provided e-catalogues that include only part of their material. Data were entered from card catalogues from some institutions. Several collections were visited and their stomiids critically reviewed. Some data were compiled from published information.

The collections described in detail below contributed to at least 1% of the data assembled in the *S_db* or own important type material. A list of the other collections that hold few midwater fish material but have regional relevance is also provided.

The valuable collections of midwater fish kept by eastern European institutions could not be easily estimated. The references to those collections in the *S_db* were compiled from published data, both regional midwater surveys and systematic studies (e.g. Bekker et al., 1975; Gushchin and Kukuyev, 1981; Kaskhin, 1982; Kukuyev, 1982; Parin and Golovan, 1976; Parin, Sazonov and Mikhailin, 1978; Novikova, 1967; Parin and Borodulina, 1996; 1997; Parin and Novikova, 1976; Parin and Pokhilskaya, 1974; Scherbachev and Novikova, 1976). The metadata summarised below about those ichthyological collections were, however, kindly provided by the curators of those institutions.

The acronyms used were those compiled from Eschmeyer (1998; http://clade.acnatsci.org/allcatfish/ACSI/museums/abbrev.html), which followed and improved the list presented by Leviton et al. (1985) and Leviton and Gibbs (1988). However, some acronyms follow the request of curators (e.g. IORAS instead of IOM or IOAN).

Some general data were obtained from the Ichthyology Web Resources (http://www2.biology.ualberta.ca/jackson.hp/IWR/index.php), BIOSIS Fish–Museums collections and catalogues (www.biosis.org/zrdocs/zzolinfo/fish_mus.htm), Biodiversity and Biological Collections Web Server (http://biodiversity.uno.edu/muse/sites.html) and FishBase (www.fishbase.org). Additional data were selected from the sites of those collections (holdings, methodologies, contacts, etc). Many institutions with e-catalogues have on-line search engines to query the database and download data.

The information provided for the collections described below are:

Name, acronym, addresses, and curator(s); symbols after the acronym**:** * collections totally ($*^1$) or partially ($*^2$) assessed; $^{\mathbf{www}}$ on-line e-catalogues; $^{\mathbf{file}}$ digital files provided by the institutions; $^{\mathbf{ref}}$ published data.

Extent: number of records or lots provided by each collection in relation to the total number of records assembled in the *S_db* **(**percentage);

(Bd): number of species in relation to the total North Atlantic stomiid assemblage (142 species; percentage);

Type material: (only for Stomiidae): + + + many, + few;

Type catalogue: reference; only if contains Stomiidae type material;

Area covered: geographical region(s) sampled;

Dates: time interval (years) of relevant sampling programs (time interval of the entire collection);

Main cruises: cruises that supplied the material; vessel name; cruise reference and year;

Relevant references: references that contain cruise data associated with the material, or otherwise information about programs and samples.

Comments: other relevant information.

Ichthyological collections of North Atlantic midwater fishes

North America

American Museum of Natural History (AMNH) [file, www]

Central Park West at 79th St., New York, New York 10024, USA
www.amnh.org/; http://research.amnh.org/ichthyology/

Curator: M. Stiassny, S. Schaefer and J. Sparks

Ext. (Bd) %: 1.9 (31.9)
e-catalogue? Yes
Type material: No
Type catalogue:

Area covered: Bermuda
Dates: 1929-31 (1910-82)
Main cruises: New York Zoological Society (NYZS), Bermuda Oceanographic Expeditions, 1929-31 (93% of the records).

Relevant references: Beebe (1931a,b, 1932a)

Comments: Intensive midwater survey made off Bermuda by C.W. Beebe under the support of the New York Zoological Society. The author used an array of ring nets (1-m diameter) fishing down to the bathypelagial during day. The AMNH possesses an important collection of larvae of midwater fish species. The USNM retains Beebe's (e.g. 1933) type material (Mead, 1958), many of which have been synonymised. The California Academy of Sciences (CAS) holds part of the fishes caught during the NYZS Expeditions. On-line catalogue. Partner of the FISHNET and FishBase initiatives. Poss and Collett (1995) index: 49

Huntsman Marine Science Centre, Atlantic Reference Centre (ARC) *[2, www]

St. Andrews, New Brunswick E0G 2X0, Canada
http://www.huntsmanmarine.ca/arc.htm

Curator: Lou van Gulpen

Ext. (Bd) %: 7.6 (43.3)
e-catalogue? Yes
Type material: No
Type catalogue:

Area covered: NW
Dates: 1979-89 (1954-
Main cruises: R/V *Alfred Needler* (1986-89); R/V

Atlantic, Gulf Stream Slope Water, Newfoundland Basin	92)	*Belogorsk* (1979); R/V *Gadus Atlantica* (1986); R/V *Ekliptika* (1979); *Hakurei Maru* (1979): 79%. More collections from 53 cruises

Relevant references: McKelvie (1985a,b); McKelvie and Haedrich (1985); Themelis (1996);

Comments: Most of the midwater fishes at ARC were collected by the Department of Fisheries and Oceans (DFO) and Dalhousie University, Halifax (R. Halliday and D.E. Themelis). This reference centre holds an important collection of Slope Water fish larvae, assembled in the ARC ichthyoplankton database. The institution is partner of the Census of Marine Life/ OBIS project “Gulf of Maine Biogeographic Information System” (GMBIS) (http://gmbis.marinebiodiversity.ca/aconw95/aconscripts/gmbis.html). The ARC e-catalogue supports the on-line mapping facility of GMBIS and the catalogue can be downloaded from the GMBIS site, but cruise data need to be requested from ARC. The collection is partner of the FishBase initiative. Poss and Collett (1995) index: 105.

California Academy of Sciences, Department of Ichthyology (CAS)$^{file,\ www}$

875 Howard St., San Francisco, California 94103, USA
http://web.calacademy.org/research/ichthyology/

Curator: Tomio Iwamoto, William Eschmeyer; Jon Fong, Dave Catania

Ext. (Bd) %: 4.0 (12.1)	**e-catalogue?** Yes	**Type material:** No	**Type catalogue:**
Area covered: Bermuda	**Dates:** 1929-31 (1928-34)	**Main cruises:** New York Zoological Society (NYZS) Bermuda Oceanographic Expeditions, 1929-31 (98% of the records).	

Relevant references: Beebe (1931a,b, 1932a)

Comments: CAS holds fishes caught by C.W. Beebe, J. Tee-Van, et al. during the NYZS Bermuda Expeditions. The former NYZS material was split between CAS, SU, AMNH and USNM. The fish collection from the Stanford University (SU) is now at CAS, and the lots are still catalogued as SU. The Smithsonian collection retains Beebe’s (e.g. 1933) type material (Mead, 1958). CAS (and SU) keep lots only from selected groups of fishes (i.e. Stomiidae subfamilies). The collection contains midwater fishes from the South Pacific. The on-line e-catalogue provides full occurrence and cruise data in tables; data files can be requested. Partner of the FISHNET and FishBase initiatives. Poss and Collett (1995) index: 43.

Field Museum of Natural History, Division of Fishes (FMNH)^{www}

Roosevelt Road at Lake Shore Dr., Chicago, Illinois 60605, USA
http://www.fieldmuseum.org/research_collections/zoology/default.htm

Curators: B. Chernoff, M. Westneat, M.A. Rogers, K. Swagel

Ext. (Bd) %: 1.6 (29.8)	**e-catalogue?** Yes	**Type material:** No	**Type catalogue:**

Area covered: Bermuda, Gulf of Mexico

Dates: 1948; 1957; 1959-60 (1948-1964)

Main cruises: R/V *Caryn* (1948); R/V *Oregon* (1957): 42%. More sparse collections from 34 other cruises

Relevant references: Grey (1955)

Comments: Most of the collections deposited in FMNH are bycatch of fishery biology surveys directed at deep-water shrimp, using bottom trawls. The FMNH holds some midwater material from the Indian Ocean and North Pacific. On-line e-catalogue; full biological and cruise data can be downloaded. Partner of the FISHNET and FishGopher projects. Poss and Collett (1995) index: 51

Gulf Coast Research Laboratory Museum (GCRL) ^{www}

PO Box 7000, Ocean Springs, Mississippi, 39564-7000, USA

http://www.coms.usm.edu/museum/index.php

Curators: C. Aadland, S. Lecroy

Ext. (Bd) %: 0.8 (12.1)

e-catalogue? Yes

Type material: No

Type catalogue:

Area covered: Mediterranean; Iceland

Dates: 1967; 1972 (1951-80)

Main cruises: R/V *Lynch* (MEDWIN, 1972); R/V *Gilliss* (1967): 75%. More sparse collections from 14 other cruises

Relevant references:

Comments: Partner of the FISHNET and FishBase initiatives. Poss and Collett (1995) index: 77

Anon., 2000. Fish collection database of the Gulf Coast Research Laboratory (GCRL). Presently, the ichthyological collection of the Gulf Coast Research Laboratory Museum has no web page.

Harvard University, Museum of Comparative Zoology (MCZ) *$^{2, file, www}$

USA, Cambridge, Massachusetts 02138

www.mcz.harvard.edu/fish/

Curators: K. Liem, K. E. Hartel

Ext. (Bd): 36.3 (80.9)

e-catalogue? Yes

Type material: +

Type catalogue:

Area covered: Atlantic

Dates: 1962-86 (1878-1999)

Main cruises: R/V *Atlantis II* (1964, 1966, 1969, 1970, 1972, 1973, 1978, 1981); R/V *Chain* (1961, 1963; 1965, 1966, 1967, 1968, 1972); R/V *Oceanus* (1977, 1978, 1979, 1982, 1984, 1986); R/V *Knorr* (1971, 1974, 1977); R/V *Cape Haterras* (1992); R/V *Blue Dolphin* (1963); R/V *Albatross IV* (1975); *Cape Florida* (1984); R/V *Columbus Iselin* (1983, 1993);

R/V *Atlantis* (1954); R/V *Endeavor* (1977); R/V *Delaware II* (1999): 76%. More collections from 132 other cruises

Relevant references: Backus and Craddock, 1977; Craddock et al., 1987

Comments: The MCZ holds the largest collection of midwater fishes from the Atlantic Ocean. It cares for the material collected by the Woods Hole Oceanographic Institution (WHOI), and other New England institutions throughout the 20th century. The extensive Atlantic pelagic zoogeography program (Backus et al., 1977, and references therein) provided most of the material. The MCZ/ WHOI midwater fish collection covers mainly the upper layers of the Atlantic mesopelagial. Although the collection holds few midwater fish type material, it supports major research on fish systematics. Recently the MCZ received the fishes sampled around the Bear Seamount (NW Atlantic) (e.g. Moore et al., 2001, 2002, 2004). The collection also preserves Indian Ocean and eastern South Pacific mid-water fishes. The MCZ Larval Fish Archive compiles relevant data about larvae of midwater species. The MCZ e-catalogue is the most complete and accurate dataset linking cruise to biological data. Partner of the FISHNET and FishGopher projects. Poss and Collett (1995) index: 49

University of Florida, Natural History Museum (UF) *[1, file, www]

Gainesville, Florida 32601, USA
www.flmnh.ufl.edu/fish/

Curator: George H. Burgess, James S. Albert, Robert Robins

Ext. (Bd) %: 2.4 (46.1)

e-catalogue? Yes

Type material: +

Type catalogue:

Area covered: off Florida, Caribbean, Gulf of Mexico, Gulf of Guinea

Dates: 1962-66 (1952-89)

Main cruises: R/V *Pilsbury* (1964-66). More collections from ca. 80 cruises

Relevant references:

Comments: Good coverage of the Atlantic tropical. Despite its relatively small size the collection holds an important diversity of Stomiidae. The collection includes the midwater fish previously housed by the University of Miami Marine Laboratory (UMML), and by the National Marine Fisheries Service, at Miami and Pascagoula. On-line e-catalogue; full biological and cruise data downloadable. The UF is partner of the FISHNET initiative. Poss and Collett (1995) index: 63

Smithsonian Institution, National Museum of Natural History (USNM) *[2, www]

Washington, D.C. 20560, USA

www.nmnh.si.edu/vert/fish.html

Curators: V.G. Springer, J.T. Williams, G.D. Jonshon, L. Parenti, S.L. Jewett

Ext. (Bd): 14.5 (85.8)

e-catalogue? Yes

Type material: + + +

Type catalogue:

Area covered: Atlantic; mainly NW Atlantic; Mediterranean.

Dates: 1960-73 (1879-1989)

Main cruises: R/V *Anton Dohrn* and R/V *Frederik Hensen*, Sargasso Sea Expedition, 1979; Ocean Acre cruise series: R/V *Delaware II* (1971); R/V *Sands* (1969-72); R/V *Trident* (1967-68). R/V *Oregon II* (1969, 1970); R/V *Albatross IV* (1969); R/V *Atlantis* II (1970); R/V *Cape Florida* (1984); R/V *Oceanus* (1977); R/V *Gilliss* (1968); R/V *Suncoaster* (1985); R/V *Walther Herwig* (1971): 41%. More collections from 220 cruises

Relevant references: Goodyear et al. (1972); Krueger et al., (1976, 1977); Gibbs and Krueger (1987); Post (1987)

Comments: The USNM holds the very important collections from the Bermuda Ocean Acre Program and from several other programs in association with e.g. the U.S. Office of Naval Research (e.g. Mediterranean Biological Studies, JOAST or Dumpsite 106 Evaluation). Also it includes material from the USFWS. A considerable amount of material came from cruises carried out by other institutions, where the majority of the fish lots are preserved (e.g. ZMH/ ISH Sargasso Sea Expedition, 1979). The stomiids fishes from USNM supported the most relevant Stomiidae systematics reviews carried out by Robert H. Gibbs. The USNM is partner of the FISHNET initiative. Poss and Collett (1995) index: 34.

Yale University, Peabody Museum of Natural History (YPM) [www, file]

170 Whitney Avenue, New Haven, Connecticut 06511, USA

www.peabody.yale.edu/collections/ich/

Curator: J. Gauthier; E. Vrba

Ext. (Bd): 0.9 (31.9)

e-catalogue? Yes

Type material: + +

Type catalogue: Moore and Boardman (1991)

Area covered: Bermuda; Off Iberia Peninsula

Dates: 1927 (1925-95)

Main cruises: R/V *Pawnee* (1927); unidentified vessel/ cruise (1959): 63%. More collections from 12 cruises

Relevant references: Parr, 1937

Comments: The collections preserves the important Stomiidae type material (as for other midwater fish taxa) designated by Albert E. Parr (e.g. 1927). A collection of mesopelagic fishes from off southwest Portugal was donated to the YPM by Professor Talbot Waterman. Poss and Collett (1995) index: 94

Europe

Natural History Museum, London (BMNH) $^{\text{www, file, ref, *2}}$

UK, Cromwell Road, GB- London SW7 5BD
http://www.nhm.ac.uk/zoology/fish/
Curators: Olivier Crimmen, Colin McCarthy, Patrick Campbell, James Maclaine

Ext. (Bd): >11.8 (>65.2)
e-catalogue? Yes
Type material: + + +
Type catalogue:

Area covered: NE Atlantic, Atlantic transects
Dates: 1921-22; 1981; 1965; (1873-1995)
Main cruises: R/V *Margrethe* (1913), R/V *Dana* (1921-22); R/V *Cirolana* (1973); about 16 IOS/ SOC cruises from 1965 to 1985 and 1994, 1997, (e.g. R/V *Discovery* SOND Cruise, 1965]; R/V *Discovery* [Azores Front, 1981]) and other midwater fish collections from sparse cruises in the Northeast Atlantic.

Relevant references: Schmidt, 1929; Anon., 1934; Foxton, 1969, Angel, 1989

Comments: The Natural History Museum holds historical material from "*Dana*" Expeditions and earlier "*Discovery*" cruises (1925-37; 1950-61). It contains also the "Discovery Collection" midwater fishes collected by the former Institute of Oceanographic Sciences (IOS, Wormley). The IOS kept each fish collection (from a net-haul) unsorted, unidentified and uncatalogued. However, the George Deacon Division of the Southampton Oceanography Centre (http://www.soc.soton.ac.uk/GDD/) holds a database with biological and cruise data from the IOS "*Discovery*" and "*Challenger*" oceanic surveys (Hargreaves, 1990). After 2000, the BMNH fish collection team has been involved in sorting, re-identification, cataloguing and databasing of the IOS material. Only part of that material is already incorporated. After the curation of the totality of the IOS/ BMNH midwater fish collection it merits a comprehensive systematic survey. The quality of the sampling methodologies and the extensive geographical coverage of the eastern North Atlantic give to this collection an extra value. The institution also holds midwater fishes from Indian and Pacific Oceans. An e-catalogue of the BMNH ichthyological collection is in progress. The existing entries can be downloaded as a text file from the museum web page. Partner of the FishBase initiative.

University of Bergen, Museum of Zoology (ZMUB) $^{\text{ref ; e-cat}}$

Muséplass 3, N-5007 Bergen, Norway
Curator: Ingvar Byrkjedal

Ext. (Bd): 0.8 (14.9)
e-catalogue? Yes
Type material: +
Type catalogue:

Area covered: Atlantic longitudinal transects; Mid Atlantic Ridge (Iceland to Azores)

Dates: 1910, 2004

Main cruises: *Michael Sars* North Atlantic Deep-Sea Expedition (1910); "*G.O.Sars*" MAR-ECO Cr 2004

Relevant references: Murray and Hjort, 1912

Comments: The collection has historical interest. The material supported intense research published in the classical reports on the Scientific Results of the "*Michael Sars*" North Atlantic Deep-Sea Expedition 1910. Presently the ZMUB holds the fishes (midwater and demersal) collected during the 2004 "*G.O.Sars*" cruise under the MAR-ECO initiative (www.mar-eco.no; Bergstad and Godø, 2003). The collection has an on-line e-catalogue, but only number of lots per species can be retrieved. The unique Stomiidae type held by ZMUB was dried up

University of Hamburg, Zoologisches Museum (ZMH/ ISH) *[2]

Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany
www.rrz.uni-hamburg.de/ichthyo/welcome.htm
Curator: Horst Wilkens, F. Grudun

Ext. (Bd): 9.4 (79.4)

e-catalogue? part

Type material: +

Type catalogue: Krefft (1978, 1987)

Area covered: Atlantic; NE Atlantic, Mid-Atlantic-Ridge, Sargasso Sea; latitudinal Atlantic transects

Dates: 1964-86 (1950-2000)

Main cruises: R/V *Anton Dohrn* and R/V *Frederik Hensen* - Sargass Sea Expedition, 1979; R/V *Walther Herwig* (Hatton Bank Cruise, 1986); R/V *Walther Herwig* (1968); R/V *Walther Herwig* (Overflow Expedition, 1973); R/V *Walther Herwig* (Mitt. Atl. Rü. Expedtion, 1982); R/V *Walther Herwig* (1971); R/V *Walther Herwig* (1966); R/V *Walther Herwig* (1964): 73%. More collections from 44 other cruises

Relevant references: Krefft, 1966; Post, 1987

Comments: The ZMH holds the midwater fish collected and formerly preserved by the Institute für Seefischerei (ISH), Hamburg. The collection includes very large midwater fish specimens because most of the material was sampled by large pelagic commercial trawls (Engel 1600). Krefft (1974, 1976) analysed the biogeography of the fishes sampled. Many specimens caught by the ISH surveys are deposited in the USNM and ZMUC. The museum holds an important collection of midwater fish fauna from South Atlantic. The Institut für Seefischerei compiled a database of its former fish collections. The ZMH e-catalogue is in progress. Both databases feed international initiatives, namely FishBase. The midwater fishes sampled by Kothaus (1972) and catalogued under the RBB acronym were incorporated in the ZMH.

Museé National d'Histoire Naturelle (MNHN) [www, file]

Laboratoire d'Ichthyologie Générale et Appliquée, 43 rue Cuvier, F-75231 Paris Cedex 05, France
http://www.mnhn.fr/museum/foffice/science/science/ColEtBd/collectionsMuseum/collectionSci.xsp;
http://ichtyonb1.mnhn.fr/gicim/searchgicim.cfm
Curator: J.-C. Hureau; G. Duhamel; N. Bailly; P. Pruvost

Ext. (Bd): 0.5 (17.7)
e-catalogue? Yes
Type material: +
Type catalogue: Bertin, 1940

Area covered: NE Atlantic
Dates: 1969 (1812-1987)
Main cruises: R/V *Jean-Charcot*, Noratlante Expedition, 1969: 20%. More sparse collections from 35 other cruises

Relevant references:

Comments: This important collection, the oldest in the world, holds few midwater fish from the North Atlantic. The GICIM (*Gestion Informatisée des Collections Ichtyologiques des Musées d'histoire naturelle de France*) assembles the ichthyological e-catalogue of the museum (Hureau, 1991). The GICM includes the type material of the Musée Océanographique de Monaco (MOM) and other French ichthyological collections. The MNHN preserves midwater fish fauna from the southeastern Atlantic off Namibia and Angola (e.g. Blache, 1960, 1962, 1964a), from the Indian (e.g. off Madagascar, Kerguelen, Amsterdam Islands) and Pacific (e.g. off New Caledonia, Marquise Islands). The museum is partner of the FISHNET and FishBase initiatives.

Museé Oceanographique du Monaco (MOM) [ref]

Avenue Saint-Martin, MC-98000, Monaco
http://www.oceano.mc/sommaire.htm
Curator: C. Carpine

Ext. (Bd): 0.5 (13.5)
e-catalogue? No *
Type material: + +
Type catalogue: Belloc, 1949

Area covered: NE Atlantic, Mediterranean
Dates: 1887-1913
Main cruises: *Princess Alice II* (1910) and *Hirondelle II* (1911-13)

Relevant references: Richard, 1934

Comments: The MOM has historical and taxonomic interest. It preserves the types caught during the pioneer "Campagnes Oceanographiques du Prince Albert I du Monaco" (1885-1914). Those midwater fishes supported major research on systematics. The museum web page does not have any information concerning the ichthyological collection. * However, the data on MOM type material is available at the GICIM (http://ichtyonb1.mnhn.fr/gicim/searchgicim.cfm).

National Museums of Scotland, Natural History (NMSZ) *[2]

Chambers Street, Edinburgh EH1 1JF, Scotland
http://www.nms.ac.uk/home/index.asp?m=4ands=1andss=2.1

Curator: Geoff N. Swinney

Ext. (Bd): 3.0 (33.3)
e-catalogue? No
Type material: No
Type catalogue:

Area covered: Madeira and Gulf of Biscay
Dates: 1983-82
Main cruises: R/V *Challenger* (1983); R/V *Frederick Russel* (1982)

Relevant references:

Comments: The NMSZ keeps mainly material caught by three IOS cruises designed to test the influence of electric light on the captures of mesopelagic organisms (Clarke and Pascoe, 1985; Swinney et al., 1986). The collection holds some unsorted material from off Madeira and some lots of midwater fishes from the Indian Ocean. The NMSZ is not catalogued.

University of Copenhagen, Zoological Museum, (ZMUC) *[2]

Danmark, Universitetsparken 15, DK-2100 Copenhagen
http://www.zmuc.dk/

Curator: Jørgen Nielsen; Peter R. Møller

Ext. (Bd): 13.3 (80.1)
e-catalogue? Part
Type material: + + +
Type catalogue: Nielsen (1974)

Area covered: Atlantic; NE Atlantic; Greenland
Dates: 1909-13; 1920-22; 1928-30 (1883-1998)
Main cruises: *Dana* Expeditions I, II, III (1920-22); *Margrethe* (1913); *Dana II* Expedition Round the World (1930); *Dana II* Expedition 1931; *Thor* 1909-10; R/V *Walther Herwig* (1968); R/V *Walther Herwig* (Mitt. Atl. Rü. Expedtion, 1982): 67%. More collections from 131 cruises

Data quality:
Relevant references: Schmidt, 1929; Anon., 1934, Tåning, 1944

Comments: The former ZMUC holds the most important historical collection of midwater fish fauna. The material was sampled during the prolific "*Dana*" Expeditions. Those expeditions sampled the North Atlantic (1920-22; 1931, 1934, 1966) and around the World (1928-1930), and provided large numbers of unknown species. The material supported many of the studies that shaped the systematics of midwater fishes; they were published mainly in the "Dana Reports". The ZMUC still retains unworked *Dana* material, both larvae and adults from various oceans. The ZMUC also cares for mesopelagic fishes from the *Galathea* Expedition 1950-52, from recent fishery biology cruises in Greenland waters, and from pelagic surveys made at Canaries (Bordes et al., 1999; Wienerroither, 2003). The institution owns thousands of samples of ichthyoplankton of midwater fish species; most of those collections are identified to families. The e-catalogue is in progress. The COBICE program supports research programs to be developed in the collection. The ZMUC is partner of the FishBase initiative. Since January 2004, the Zoological Museum is a department of the Natural History Museum of Denmark (Statens Naturhistoriske Museum), University of Copenhagen.

Eastern Europe

AtlantNIRO, Atlantic Research Institute of Marine Fisheries and Oceanography, 5, D. Donskoy St., Kaliningrad, 236000, Russia. Curator: Efim Kukuev

Comments: The AtlantNIRO holds the fishes sampled during exploratory expeditions promoted by the institution. The fish collections from the following geographical areas are maintained: North-Atlantic Ridge (60º - 45º N; 1975-76, 1978, 1981 and 2003); Irminger Sea (1999, 2003); Rockall Trough (2001, 2003); Corner Seamounts (1976-78, 1986, 2001); Gulf Stream (1981-83, 1989); and seamounts to the north and south of the Azores. The research vessels "*Atlant*", "*Bakhchisaray*", "*Coryphena*", "*Pioneer of Latvia*" and "*Evrica*", among others, were employed in those expeditions. The holdings of meso- and bathypelagic fishes account for more than 20,000 specimens and 200 species caught during ca. 18 expeditions. The pelagic and the demersal fishes are inventoried, labelled, fixed in formalin- and stored unsorted in ca. five hundred 20-25 litre glass vessels. The collection has no web page, but see http://www.atlantniro.ru/en/. *Relevant references:* Guschin and Kukuev, 1981; Kukuev, 1982, 1984, 1991, 2002, 2004; Kukuev et al., 2000; Kukuev and Trunov, 2002.

IORAS, P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia (www.sio.rssi.ru/). Curator: S. Evseenko

Comments: The IORAS (former IOAN) accomplished many pelagic surveys in the Atlantic, Indian and Pacific, but the investigations concentrated mainly in the latter two oceans. The IORAS holds North Atlantic midwater fauna caught by the following cruises: "*Vityaz*" cr. 65, (1979, Mediterranean); "*Vityaz 1*" cr. 2 and 9 (1981, Caribbean Sea; 1985, eastern Atlantic); "*Academician Kurchatov*", cr. 1, 4, 14, 31 (1967, eastern Atlantic; 1968, western Atlantic; 1973, Caribbean and Gulf of Mexico, 1980, central North Atlantic); "*Mendeleyev*", cr. 1 (1969, western Atlantic); "*Vavilov*", cr. 1 (1988, northeast Atlantic); "*Ioffe*", cr. 3 (1990, northeast Atlantic). In total more than 600 pelagic fish samples were obtained in ca. 400 stations surveyed during those 10 cruises. In general, each sample is preserved unsorted in a large jar.

Possibly the IORAS also holds some of the material caught during the acoustic surveys carried out by "*Petr Lebedev*" Cr 1, 2, 4, 6 (1961, eastern tropical Atlantic; 1962, western tropical atlantic; 1964, subtropical Atlantic; 1967, northeast Atlantic, respectively).

ZIN, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (http://www.zin.ru/anim_e.htm); **Curator(s):** Natalia Chernova

Comments: This collection received material from investigations undertaken by the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Murmansk, Russia). It holds one Stomiidae type specimen. No more information is available about that collection.

ZMMU, Zoological Museum of the Moscow State University, Moscow, Russia. (http://zmmu.msu.ru/s_p_m.htm). **Curator**: Katrina Vasil'eva

Comments: The ZMMU keeps a few Stomiidae syntypes. No more information is available about that collection.

IBSS, Institute of Biology of the Southern Seas, National Academy of Sciences of Ukraine; Sevastopol, Crimea, Ukraine (www.ibss.iuf.net); **Curator:** A. Boltachev

Comments: the collections include material caught by the institution during exploratory surveys. The investigations focused on the pelagic ichthyocenoses of the Eastern Tropical Atlantic (25ºN; 10º N – 40º S to 24º W) and Indian Ocean. The IBSS holds midwater fishes caught by the following pelagic surveys (research vessel, date): "*Professor Vodyanitsky*", (1981, 1982, 1987); "*Vozrozhdeniye*" (1980); "*Novoukrainka*" (1981); "*Ichthyandr*" (1982); "*Titanit*" (1984). The holdings of mesopelagic fish comprise 304,000 specimens produced by 332 field samples (61% night time). The collection is inventoried/ catalogued but not computerised.

Relevant references: Boltachev, 1987, 1992, 1994; Boltachev et al., 1988; Ovcharov, et al., 1990; Ovcharov and Boltachev, 1990

SFI, Sea Fisheries Institute in Gdynia, Poland. (www.mir.gdynia.pl)

Comments: The SFI does not preserve any formal ichthyological collection. The assortment includes several hundred lots of myctophids and sternoptychids. The extant material was collected during Polish midwater surveys to the northeastern Atlantic, including the Mid-Atlantic Ridge, on board the R/V "*Profesor Siedlecki*" between 1975 and 1987. It holds also fish from other areas of the Atlantic and from the Southern Ocean. There is some unsorted material and an extensive myctophid otolith collection. The SFI is inventoried but not catalogued and the access is limited.

Other collections

CBR (CSIC-ICM)$^{www\ *}$, Instituto de Ciencias del Mar, Colecciones Biológicas de Referencia, Barcelona, Spain. http://www.icm.csic.es/rec/gim/cbr/colec.htm. **Curators:** D. Lloris, C. Allué.

Comments: western Mediterranean and eastern tropical Atlantic. Extent (Bd): 0.2% (5.0%). The CBR holds few lots of midwater fish fauna from off Namibia. Partner of FishBase initiative.

DOP, University of the Azores, Department of Oceanography and Fisheries, Azores, Portugal. www.horta.uac.pt. **Curator:** J. Gonçalves, F.M. Porteiro

Comments: Azores region. Extent (Bd): 0.3% (9.9%). An e-catalogue is in progress. At present the collection has no web page.

KU $^{www\ *}$ University of Kansas, Museum of Natural History, Kansas, USA. http://nhm.ku.edu/fishes/. **Curators:** E.O.Wiley, J.T. Collins

Comments: western Atlantic. Ext. (Bd) ^{est}: 0.1% (7.1%). KU holds an important bank of muscle tissue of deep-sea fishes, namely from Atlantic Stomiidae (34 samples of 12 spp.) and other midwater species and families (searchable at KU web page). The institution leads the FISHNET initiative and is partner of FishBase. Poss and Collett (1995) index: 85

MMF$^{e\text{-}cat}$, Museu Municipal do Funchal, Madeira, Portugal. http://www.cm-funchal.pt/actividades/ciencia/portugues/mm01000.html. **Curator:** M. Biscoito

Comments: Madeira region. Extent (Bd): 0.3% (14.2%). The MMF holds an additional collection of midwater fish from around Madeira. Many samples were obtained from stomachs of black-scabbard fish (*Aphanopus carbo*). Relevant references: Maul, (1948, 1956)

RMNH, Naturalis, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands. www.naturalis.nl. **Curator:** M.J.P. van Oijen.

Comments: The RMNH holds a small midwater fish collection caught during the CAN-CAP Expeditions. The Expeditions surveyed the waters around the Canary, Cape Verde and Azores Islands. The samples were taken by a modified Isaacs-Kidd-Midwater Trawl (HPN, Hamburg Plankton Net; 27 hauls), a 1-m diameter ring trawl (75 hauls) and a neuston net (2 hauls). Most of the material is preserved, unsorted and unidentified. No digital catalogue is available. The SYNTHESYS program supports research in the RMNH. References: De Groot and Nijssen., 1971, Van der Land (1987), Boeseman, 1997.

ROM$^{e\text{-}cat}$, Royal Ontario Museum, Department of Ichthyology and Herpetology, Toronto, Canada. www.rom.on.ca/biodiversity/cbcb/. **Curators:** R. Winterbottom, M.E. Burridge, E. Holm.

Comments: Northwestern Atlantic off Canada. Ext. (Bd): 0.5% (5.7%). The midwater fish collections were caught by the R/Vs "*Lawrence*" and "*Gadus Atlantica*" in 1966 and 1981, respectively. The collection has no web page. The data from the e-catalogue should be required to staff or downloaded from FISHNET or FishBase initiatives. Poss and Collett (1995) index: 63

SIO^{www}, University of California, Scripps Institution of Oceanography, Marine Vertebrates Collection, USA. http://collections.ucsd.edu/mv/index.cfm. **Curators:** P.A. Hastings, R.H. Rosenblatt, H.J. Walker, C. Klepadlo, (cklepadlo@ucsd.edu; hjwalker@ucsd.edu; phastings@ucsd.edu)

Comments: Caribbean Sea (25ºN, 77ºW). Ext. (Bd): 0.3% (11.3%). Midwater fish caught mainly by the R/V "*Marstar*" in 1981-82. The SIO preserves mainly midwater fishes from the eastern Pacific and Hawaii. Many surveys made with the Isaacs-Kidd Midwater Trawl, a gear developed at SIO. The institution preserves an important collection of type material (e.g. 30 Stomiidae types from Pacific). Partner of the FISHNET and FishBase initiatives. Poss and Collett (1995) index: 59

VIMS $^{www\ *}$, Virginia Institute of Marine Science, Gloucester Pt., Virginia, USA. www.vims.edu/ich_coll.html. **Curator:** J.A. Musick, P. Gerdes (jmusick@vims.edu)
Comments: Western North Atlantic (Mid-Atlantic Bight, Blake Plateau, Norfolk Canyon, etc). Extent (Bd): 0.8% (17.0%). Lack of cruise data associated with many midwater fish holdings, which were caught mainly by bottom trawls. Poss and Collett (1995) index: 117

ZMA, University of Amsterdam, Zoological Museum Amsterdam, the Netherlands. www.science.uva.nl/ZMA/vertebrates/Fishes.htm. **Curator:** Isaäc Isbrücker (isbruecker@science.uva.nl)
Comments: The institution promoted the five cruises part of the Amsterdam Mid North Atlantic Plankton Expedition (1980-83; Van der Spoel, 1981, 1985; Van der Spoel and Meerding, 1983). The extent and the preservation status of the midwater fish collections sampled during those expeditions are not known. The SYNTHESYS program supports visits to ZMA.

ZMHU, Museum für Naturkunde der Humboldt-Universität, Zoologisches Museum, Berlim, Germany. http://www.museum.hu-berlin.de/home.asp?lang=1. **Curators:** P. Bartsch, C. Lamour; peter.bartsch@museum.hu-berlin.de
Comments: The ZMHU holds the midwater fish collections and the type material described by P. Pappenheim and by A. Brauer, caught during the Deutschen Sudpolar Expedition (1901-03) and the Tiefsee-Expedition (R/V "*Valdivia*" 1898-99), respectively. Only few samples were taken at the North Atlantic. The exact extent of the collection was not assessed. Computerization is in progress.

The University of South Florida keeps an orphan collection of midwater fish fauna from the Gulf of Mexico obtained during a large term program on midwater ecology. (T. Sutton, Harbor Branch Oceanographic Institute, pers. comm., 2004).
Other ichthyological collections not listed in the main section of this study: MZUF, Universita di Firenze, Museo Zoologico de la Specola, Firenze, Italy; NMW, Naturhistorisches Museum, Wien, Austria; NRMS, Naturhistoriska Riksmuseet, Stockholm, Sweden; SAM, South African Museum, Cape Town, South Africa.

Conclusions

North American vs. European collections

Sixteen ichthyological resource centres hold important midwater fish collections from the North Atlantic: 9 are North American (1 Canadian), 7 Western European and 4 Eastern European. They represent a very small proportion of the 118 and 123 North American and European ichthyological collections described by Poss and Collette (1995) and Kottelat et al. (1993), respectively. According to Poss and Collette (1995), the American centres here reported were amongst the larger in that continent and they classified them as international (AMNH, CAS, FMNH, MCZ and USNM), national (UF), regional (GCRL) and other important collections (ARC, YPM). Since that time, the UF probably attained the rank of an international centre and the ARC clearly improved its Poss and Collette index. The European collections that hold midwater fish fauna are also amongst the most important in that continent and in the world. Kottelat et al. (1993) did not rank or compared the fish collections reported. The 10 other institutions holding modest numbers of midwater fish are both American (KU, SIO, VIMS and ROM) and European (CBR, DOP, MMF, RMNH, ZMA).

Collection size: number of lots and specimens (Fig. B.1a,b)

The MCZ has by far the largest collection of midwater fishes of the North Atlantic, both in numbers of lots and specimens. Most probably, the BMNH ranks as the second largest collection holding this group of fishes, but the material of that institution is still being processed and catalogued. The USNM, ZMUC, ZMH/ ISH and ARC follow in terms of importance. These six collections comprise more than 80% of the Stomiidae entries. The USNM holds more lots than the other collections, but ranks sixth after ARC if numbers of stomiid specimens are considered. This is probably because the USNM received many stomiid lots from surveys conducted by other institutions (e.g. ISH, WHOI). The CAS, NMSZ, UF, AMNH, and FMNH are intermediate collections both in terms of stomiid lots and specimens. In general their individual holdings represent between 1% and 5% of the total of stomiids inventoried. The relevance of the MOM and YPM is mainly historical.

The real extent of North Atlantic midwater fish held by the Eastern European collections is unknown. Five hundred lots distributed among 79 North Atlantic Stomiidae species were retrieved from Russian literature (Ext.: 2.5%), though the real amount of midwater fishes of those centres is much larger. At least some of those institutions (e.g. IORAS and IBSS) possibly rank among the most important ichthyological collections.

Seven of the ten collections with low numbers of midwater fishes provided 2.1% of the stomiid lots and 1.8% of the specimens. The holdings of three of them were not assessed.

Species richness (Fig. B.1c)

Because of the taxonomic work undertaken by R. H. Gibbs on stomiid fishes at USNM, this collection ranks highest in number of species. However, other large centres that hold midwater fishes from across the North Atlantic (i.e. MCZ, ZMUC, ZMH/ ISH) also possess a large proportion of the stomiid species reported to occur in the basin. The Russian collections should also contain high numbers of species; the data compiled from bibliography account for a Bd: ca. 56%. Although the UF collection has less than a half of the ARC fish holdings, it contains more stomiid species, reflecting the higher stomiid species richness of tropical seas compared to that found at the Slope Water off Canada. Other collections hold slightly less than a third of the known stomiid species diversity (NMSZ, AMNH, YPM and FMNH). The remaining collections possess low levels of species diversity (i.e. Bd: 5% - 17%).

Type specimen collections (Table 1)

The type material referenced in this survey accounts for 141 species of North Atlantic stomiids. Because "Dana" Expeditions were the first campaigns that extensively targeted the pelagic fauna of the North Atlantic, the ZMUC is the museum that holds the largest fraction of Stomiidae type- material. The material caught by the “Dana” Expeditions also constitutes the majority of the midwater fish types deposited in the BMNH. The USNM is the second-most important repository of stomiid type material; it holds Beebe’s and Welsh’s types, as well as the types used by R.H. Gibbs and co-authors to describe a large numbers of species of the genera *Eustomias* and *Astronesthes*. The YPM, MOM and ZMHU centres keep important historical midwater fish species type collections. The ZMH/ ISH and the MCZ are moderately relevant

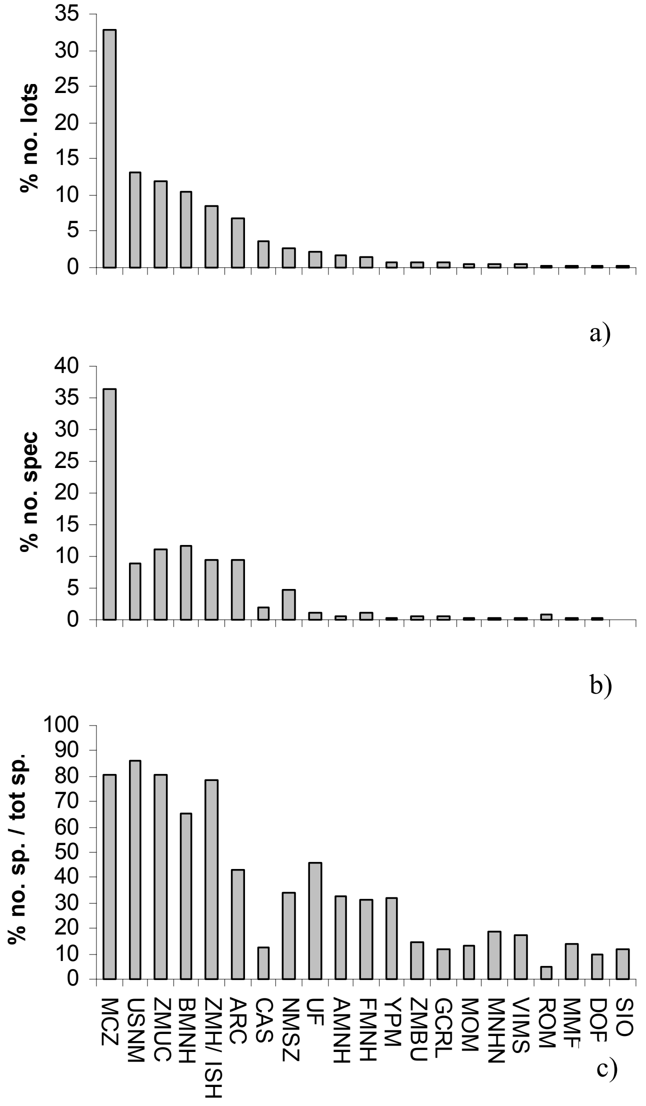


Figure B.1 Relative importance of ichthyological collections holding North Atlantic stomiid fishes in terms of (percentage) a) number of lots (records), b) number of specimens and c) number of species in relation to the total assemblage of North Atlantic stomiid species (141).

collections regarding Stomiidae type material, followed by the MNHN, ZMMU and UF (UMML). Twelve other collections care for the remaining Stomiidae types: FMNH, ZIN, IORAS, SIO, USF, ZMUB, MZUF, NMW, NRMS, SAM, AMNH and ARC.

Catalogues (cards vs. electronic)

Almost all the large and moderately large collections that maintain midwater fishes have their holdings catalogued. The exceptions are some small collections and the Russian and other Eastern Europe ichthyological collections. It is worth noting that all USA centres have complete e-catalogues available. However, the most important midwater fish collections in Europe have only part of their catalogue in an electronic format (e.g. ZMUC, ZMH/ ISH, BMNH). The data available from those American and European centres with e-catalogues can be retrieved from their web pages or from several networking initiatives, such as FishBase and FISHNET. Four of the ten small-size midwater fish collections have searchable ichthyological e-catalogues (CBR, KU, SIO

Table 1. Type material of 141 North Atlantic Stomiidae species. Number of lots per ichthyological collections (see text for acronyms). **Holotypes*** includes 1 Neotype and 5 Lectotypes and **Paratypes*** includes 22 Paralectotypes. Data source: Stomiidae database (*S_db*).

Muse_code	Holotypes*	Syntypes	Paratypes*
ZMUC	32	242	18
USNM	20		58
BMNH	9	60	16
ZMH/ ISH	9		29
YPM	13	4	1
MCZ	2		9
MOM	9		
ZMHU	7	2	
MNHN	2	30	2
ZMMU			10
UF			3
Other (12 collections)	7		10
Total	109	338	156

and VIMS). The unsorted midwater fishes kept by the ichthyological collections are not catalogued.

Quality of biological and cruise data

Often the quality of the data available in the e-catalogues needs to be improved, especially regarding cruise data associated with the biological records. This applies mainly to moderate to small-size collections, and is a relatively common feature of most of the e-catalogues considered. The MCZ has the highest standards regarding the quality of biological and cruise data. The ZMUC and the ZMH/ ISH catalogues were easily accessed by using the cruise reports of the large-scale programs that produced the bulk of their midwater fish holdings. The part of the BMNH e-catalogue relating to the IOS midwater fish needs to be matched with the database of the Deacon Laboratory (SOC, UK).

To improve the quality of the *S_db*, the museum catalogues were checked, corrected and cross-referenced, and the gaps filled with published data whenever possible (see references in the collections entries).

Special collections

Pelagic fish larvae collections are present in many institutions. The ring nets and the trawls used to catch micronekton (i.e. IKMT10, RMT8, MOCNESS10, 20) do also sample ichthyoplankton, in a varying degree of efficiency. However, as a general rule pelagic fish larvae are not identified or catalogued. Some midwater larvae kept by the MCZ were identified as a result of a fish larva program. The AMNH has a collection of the Stomiidae post-larvae described by Beebe and Crane (1939). The important ZMUC pelagic fish larvae collection needs a program directed to identify and describe the extant material. The ARC ichthyoplankton collection is one of the largest in North America, but regarding the midwater fish it is limited to the few species that occur in the Slope Water off Canada.

The CAS, USNM, FMNH, and MCZ have few numbers of cleared and stained stomiid specimens. They were used primarily by Weitzman (1967), Goodyear (1980) and Fink (1982) for phylogenetic studies. The ZMUB has an osteological reference collection that includes the skeletons of many North Atlantic midwater fishes.

Main problems

The problems and concerns of the American ichthyological collections were identified and discussed by Poss and Collette (1995). The most common problems identified in the Europeans institutions were limited funding and the deficit of curatorial staff. To computerise the entire card catalogue has been a major difficulty experienced by both the most important (e.g. ZMH/ ISH and ZMUC) and the less important collections on this continent. The lack of taxonomic expertise on the midwater fish fauna is also a major problem of many collections incorporating new holdings (e.g. BMNH). The difficulties of Eastern Europe ichthyological collections are similar, but at a more dramatic level: they have no funds to restore the collections, to acquire equipment and consumables, and to contract additional skilled personnel.

Discussion

This survey references the bulk of the sampling cruises and the existing midwater fish collections of the North Atlantic. Using the inventory of the Stomiidae fish family as a proxy, it is expected that the picture this review gives about the available collections is also valid for most other families of meso- and bathypelagic fishes. The stomiids make up a highly diverse and specialised ancient group of deep-sea pelagic fishes. The species of this family live across all oceanic basins from the equator to ca. 70º N and S. Some stomiid species are relatively abundant, but most are rare or moderate in numbers. In the North Atlantic the regional Stomiidae assemblage is relatively diverse and its components are common and frequent in the catches of all midwater micronekton surveys.

With this work, we are hoping to contribute metadata that will promote and facilitate future studies on midwater fish biogeography and biodiversity. The inventory points out to ichthyologists the majority of the large-scale North Atlantic midwater fish collections and databases that can be used to address questions related to the functioning and state of the North Atlantic pelagial. The information presented can also be relevant to international initiatives on marine biogeography/biodiversity information systems such as the OBIS and the recently developed EuroOBIS and the Distributed Generic Information Retrieval (DiGiR; http://digir.sourceforge.net/).

The main deficiency experienced by most of these collections, especially in Europe, is the urgent need to recover and care for their midwater fish holdings and fully to computerize their catalogues. This is a very costly and complex task that can be done only with the active support of the international ichthyological community, who in turn will benefit from the extremely important data that will be available. Many important collections are at risk, despite the relevance of their biological material. While these collections validate previous research, they also constitute the basis for future research.

Appendix C

The Stomiidae database (*S_db*): an overview of its structure

The Stomiidae database assembles data on stomiid midwater fish occurrences in the North Atlantic. It includes: detailed cruise data linked with the occurrences; Stomiidae systematics, morphological and ecological data; and information on the ichthyological collections that hold the material assembled.
Data sources and details about data manipulation and quality control are summarised in Appendix B and Chapter 2.

Database description (Fig. C.1)

1. MAIN table assembles basic data on species occurrence (species records). It includes the following fields: ***Rec***; ***Muse_code***; *Cat_no*; *Ref_source*; *www*; ***Taxa_code***; *Idfr*; *Syst_comm*; ***Field_code***; *Comm*, *Ref.*

Rec is the serial number (1, 2, ..., n) of the occurrences**;** it links to tables **MAIN, SIZE** and **TYPE**.

Muse_code**,** *Cat_no* and *Ref_source* relate to data sources.

Muse_code links **MAIN** to **MUSE** table (see below).

Cat_no: catalogue number attribute to a lot. Some records have more than one catalogue number because samples were shared by institutions; other lots have no catalogue number (n/cat) (see Chapter 2).

Ref_source: source data reference (published document or e-catalogues www address); often associated to ***Muse_code*** and/or *Cat_no*; it links to **REF** table.

Taxa_code: taxonomic identification of a record; often the species name (see **TAXA table** below); it links to tables **TAXA, TYPES**, **ECO** and **MORPHO**.

Idfr: name of the person who identified each record; it denotes taxonomic accuracy.

Syst_comm: comments on the systematics of non-type material records.

Comm: general information about the specimens (e.g. condition; if cleared and stained; previous catalogue number; etc.).

Field_code**:** the sampling unit; a net-haul that produced stomiids; might be associated to one or several ***Rec***, depending how much species it sampled. It links to **COLL** table.

2. COLL assembles cruise data. It includes: ***Field_code***; *Vessel*; *Cruise*; *Station*; *Lat*; *Long*; *Date*; *Year*; *Month*; *Season*; *T_out*; *T_in*; *T_fishg*; *N_&_D*; ***Gear_Code***; *D_min*; *D_max*; ***Sq_5ºx5º***.

***Field_code*:** formed by the initials of the vessel name, then by the year of capture and cruise number (if available); following station code and net code (e.g. WH-73-51:678/ 73 = "Walther Herwig" cruise 51, 1973, station 678/ 73).

Cruise: identify the cruise; coded the first part of *field_code* (WH-73-51).

Note that in the example, *station* and *field_code* are the same because only one net-haul was fished at the station. In stations performed with multi-closing devices or arrays of nets each net-haul is coded by a unique *field_code*. If station is not available a **Zn** is assigned and **n** is sequential for unknown *stations* from a cruise (e.g. LANG-90:Z1; LANG-90:Z2).

Vessel: name of the research vessel; if vessel name is unknown *field_code*, *station* and *cruise* were coded with N/A.

Lat and *Long*: geographical coordinates (in decimals of degrees) of the point where a net-haul began. For some *field_code* (<0.1%) the position was estimated, but only if the record had associated reliable topological information.

Date: the date a *field_code* was made (dd-mm-yyyy). If date is unknown then year in the *field_code*, *station* and *cruise* is replaced by 00 (e.g. N/A-00:88).

Year: four digits field.

Month: two digits field.

Season: filled with S (Spring: March, April and May), SU (Summer: June, July, August), A (Autumn: September, October and November) or W (Winter: December, January and February).

T_out: hour (00:00) when the net entered the water (non-closing net) or when a chamber or a new net was open (opening-closing devices).

T_in: hour (00:00) when the net reached the vessel or when a chamber or a net was closed.

T_fishg: time while fishing (*T_in* - *T_out*).

N_&_D: light regime; filled with D for a net-haul made during sunlight conditions; N for a nighttime haul; N&D and D&N for dawn and dusk hauls, respectively.

D_min: minimum depth of sampling (in meters); is 0 for *field_codes* made by non-closing gears.

D_max: maximum depth of sampling (in meters). For same hauls *D_max* was estimated.

Gear_code**:** identify the gear used during a *field_code*; it links **COLL** to **GEAR** table.

Sq_5ºx5º**:** number of the square in the North Atlantic geographical regular grid (5ºx5ºlatitude/longitude); numbered from north to south and from west to east; it links **COLL** to **LOCAL** table.

3. GEAR assembles gear data. It includes: ***Gear_code***; *G_type*; *G_desc*; *G_acrn*; *G_selct*; *Spcf_?*; *O_C; M_m2*; *Mesh_sz_cm*; *M_dim_m*; *Comm*; *Ref.*

Gear_code**:** hierarchical code system. First number: gear type (e.g. 1=bottom trawl; 3=micronekton trawl; 5=neuston net; 14=stomach contents); second number: gear name (e.g. 1.13 = otter trawl); third number: gear size (e.g. 2.2.6 = 1600 Engel midwater trawl); fourth number: discrete hauls by opening-closing devices (e.g. 3.5.1.1 = MOCNESS 10).

G_type: the first number of *gear_code*; 1=bottom trawl; 2=commercial midwater trawl; 3=micronekton midwater trawl; 4=unspecified midwater trawls; 5=neuston nets; 6=plankton trawl; 20=no data; and 50=other gears (i.e. drags, dredges, SCUBA, detritus samplers).

G_desc: gear name (e.g. International Young Gadoid Pelagic Trawl 100).

G_acrn: gear acronyms (e.g. IYGPT 100; IKMT 10; RMT 8).

G_selct: denotes *Gear_codes* selected for analysis (see Chapter 3).

Spcf_?: 0 = if no gear specifications are available; 1 = gear specifications available.

O_C: 0 = for non-closing devices; 1 = for opening-closing devices.

M_m2: dimension (in square metres) of the net opening.

Mesh_sz_cm and *M_dim_m* contain descriptive information about the mesh and about the dimensions of the gear, respectively. These fields are filled up only if *Gear_code* contains more than 2 numbers.

4. LOCAL assembles geographical data. It includes: ***Sq_5ºx5º;*** *Lat_5ºx5º*; *Long_5ºx5º*; *Lgh_P*; *Lgh_B*.

Sq_5ºx5º links **LOCAL** to **COLL**; (see **COLL** table).

Lat 5x5º; Long 5ºx5º: averaged geographical position (latitude and longitude in decimals of degrees) of the *field_code*s made inside each sq_5ºx5º.
Lgh_P; Lgh_B: filled with Longhurst's (1998b) eco-geographical provinces and biomes acronyms, respectively (see Chapter 2).

5. SIZE assembles biological data. It includes: ***Rec***; *No_spec.*; *Sz_min*; *Sz_max*; *Devlp_st*
***Rec*:** links **SIZE** to **MAIN** (see above).
No_spec: number of specimens in one record; *No_spec* = 1 if number of specimens is unknown.
Sz_min and *Sz_max*: size range (in mm of standard length, SL) of specimens from one record; if a *rec* includes only one fish then *Sz_max* is empty.
Devlp_st: developmental stage of the specimens: L (larvae); A (adult); J (juvenil); M or F (if adult male and female, respectively); or combinations of code (e.g. J, A if adults and juveniles in one *rec*).

6. TAXA aggregates taxonomic information. It includes: *Taxa_code*; *Taxa*; *Sub_family*; *Genus*; *Sub_genus*; *Sp_ group*; *Sp*; *Sub_sp*; *Syn*; *Comm*; *Ref*
***Taxa_code*:** the taxonomy of a record in a hierarchical code system. First number: sub-family (e.g. 4= Melanostomiidae); second number: genus (e.g. 4.13 = *Eustomias*); third number: sub-genus (e.g. 4.13.9 = *Biradiostomias*); fourth number: species group (e.g. 4.13.9.2 = group II); fifth number: species (e.g. 4.13.9.2.2 = *Eustomias dubius*).
Note that only species with accepted sub-generic classification have values > 0 on the third and fourth positions (i.e. 5.1.0.0.1 for *Idiacanthus fasciola*). ***Taxa_code*** links **MAIN** to **TAXA, TYPES**, **ECO and MORPHO** tables**).**
Taxa: taxonomic name; lower systematic level available.
Sub_family: name of the sub-family.
Genus: name of the genus.
Sub_genus: name of the sub-genus, if recognised.
Sp_ group: name of the species group, if recognised
Sp: Linnaean name of the species.
Sub_sp: name of the sub-species if recognised.

Syn: nominal synonyms recognised for species; often it contains more than one synonym; associated to a reference that links to *Ref.*
Ref includes references associated with the occurrence of a species.

7. MUSE assembles metadata on ichthyological collections (Appendix B). It includes: ***Muse_code***; *Muse_n*; *www*; *Country*; *Curator*; *Cat_type*; *Comm*; *Ref.*
***Muse_code*:** acronym of the ichthyological collection (according to Leviton et al., 1985 and Leviton and Gibbs, 1988; links **MUSE** to **MAIN**.
Muse_n: full name of the ichthyological collection.
www: web address of the ichthyological collection.
Country: country of the ichthyological collection.
Curator: name of the curator(s) and other technicians.
Cat_type: electronic vs. paper catalogue.
Comm: comments on ichthyological collection.

8. **TYPE** assembles data on North Atlantic Stomiidae type material. It includes: ***Rec***; *Taxa_code*; *Author*; *Year*; *Type*; *Comm*; *Ref*
Rec links **TYPE** to **MAIN**.
Taxa_code: links **TYPE** to **TAXA**
Author: species authority.
Year: year of species description (yyyy).
Type: holotype, lectotype, paratype, paralectotype, etc.

9. **MORPHO** assembles species morphological data (not complete).
Taxa_code links **MORPHO** to **TAXA, ECO** and **MAIN.**
Includes data about: body morphometrics; photophores (meristics and counts); barbel (morphometry and descriptive data); teeth (meristics and descriptive data); eyes (descriptive data); Swimbladder (presence or absence); colour (descriptive data).

10. ECO assembles species ecological data (not complete).
Taxa_code links **MORPHO** to **TAXA, MORPHO** and **MAIN.**

Includes data about: vertical distribution (in meters by day and night; larvae and adults); vertical migration (descriptive data); biotope (coded descriptive data); Diet and trophic guilds (coded descriptive data).

11. REF contains *Ref*; and *Ref_full*
Ref: bibliographic references; links most tables; author last name followed by year;
Ref_full: full description of a bibliographic reference.

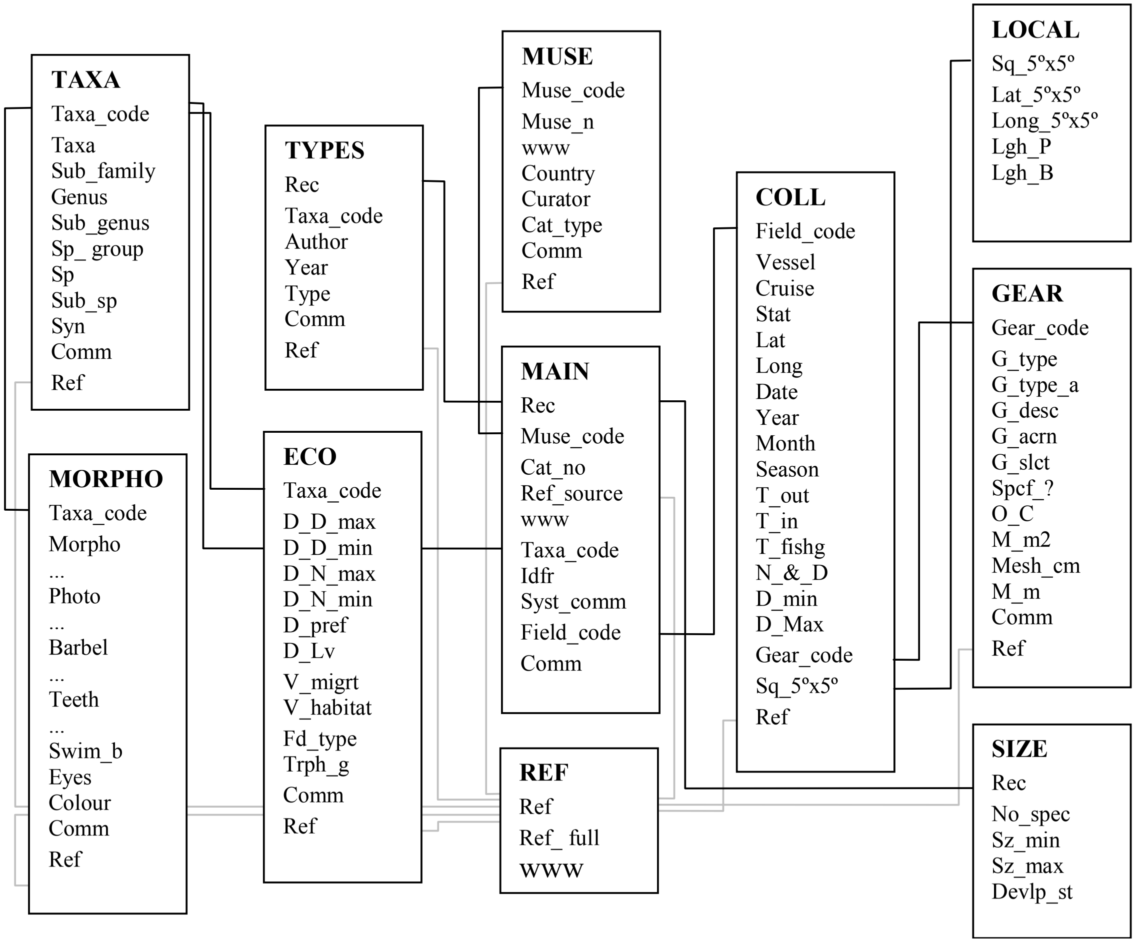


Figure C.1. Schematic structure of the Stomiidae database (*S_db*). See text for details.

Appendix D
Individual accounts on selected gears

Twenty gears were selected from the Stomiidae database to analyse cruise data, catch data and gear performance (Chapters 3 and 4). The Chapter 2 and the Appendix C give information concerning the original data associated with each gear. Technical specifications and other information concerning the selected gears are summarised in the Table 3.1 (Chapter 3). The distribution of selected gear net-hauls (= *field_codes*) by eco-geographic biomes and provinces of Longhurst (1998b) and seasons are summarised in Table D.1

The data presented for each individual gear are summarised below according the following scheme:

Gear name - acronym

References: concerning the programs carried out with the gear in consideration. **Institutions:**.that promoted those programs. **R/Vessels:** used to complete the programs (acronyms). **Programs (cruises):** full name of the programs made and codes for cruises (vessel acronym – year – cruise number). **Data amount (n):** numbers in the Stomiidae database of: net hauls; records; specimens; and species. **Data quality:** (in percentage) number of records with fish size; number of net-hauls with depth: and with time fishing: **100%**.

Geographical distribution of stations made with the gear (a dot may correspond to more than one net-haul)

Depth profile by night (n) and day (d); (← denotes the depth at 50% of the hauls)

Distribution (in percentage) of the net-hauls by night (black), day (white), dusk and dawn (grey).

Time fishing: mean (hh:mm), standard deviation and range

Table - Gear standard haul basic statistics (computed on all records reported to that gear). **avg_sz**: average standard length (mm SL); **min_sz**: average minimum size (mm SL); **max_sz**: average maximum size (mm SL); **avg_wt**: estimated average weight (g); **CPUE n**: capture-per-unit-effort in numbers (i.e. number of stomiids specimens / hour); **CPUE wt**: capture-per-unit-effort in biomass (i.e. estimated weight g/ hour); **sp/ h**: number of species per hour; **%L:** percentage of stomiid species caught in relation to the pool of stomiid species reported for each Longhurst province. See methods in Chapter 4 for details about computation of standard hauls.

Histogram of size distribution
Size classes (mm SL [standard length]):
Commercial midwater trawls: 20 mm
Micronekton and plankton trawls: 10 mm

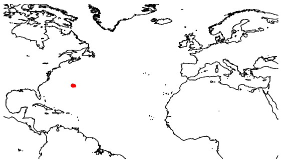
Size selectivity ogive; % caught: number of specimens caught per size classes;
logistic curve: y=1/100*(1+e^-b0(x-b1));
parameters estimated: b0 and b1

Remarks: information or comments about the gear or its use.

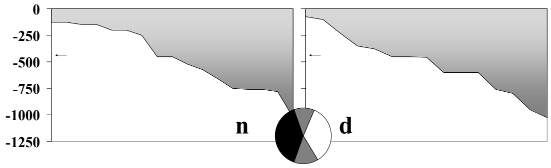
Specific account on selected gear

Engel Midwater Trawl - EMT 1400

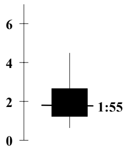
References: Gibbs & Karnella, 1987. **Institutions:** Smithsonian Institution (USNM), Washington, USA. **R/Vessels:** Albatross IV (AL4); Delaware II (DLII). **Programs (cruises):** Bermuda Ocean Acre Program (AL4-69-07; DLII-71-12 1). **Data amount (n):** net hauls: **43**; records: **307**; no specimens: **569**; no species: **63.** **Data quality:** size: **18.9%**; depth: **100%**; time fishing: **100%**.



Geographical distribution



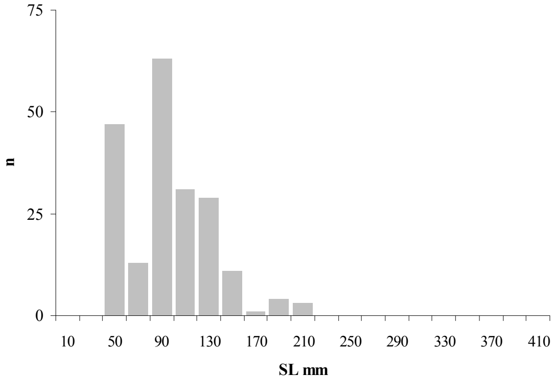
Depth profile. Night/ day net-hauls distribution



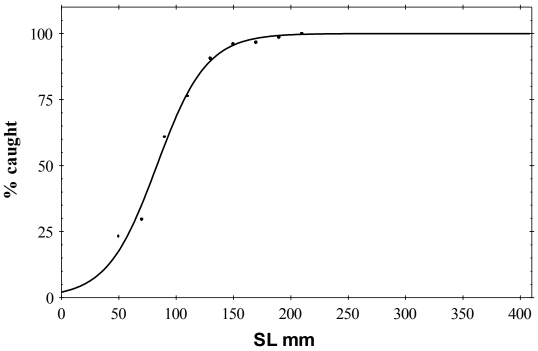
Time fishing

Standard haul basic statistics

EMT 1400	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	100.9	66.2	140.8	5.3	7.4	44.3	3.8	6.8
-95%	90.2	57.5	121.8	3.6	3.8	28.4	2.7	5.0
95%	111.6	75.0	159.8	7.0	10.9	60.3	5.0	8.5
min	56.9	41.0	63.0	0.3	0.5	1.4	0.4	1.0
max	158.9	130.0	217.4	17.7	75.0	127.3	21.8	28.2
std dev	27.0	22.1	48.0	4.3	11.5	40.3	3.8	5.7
std err	5.2	4.3	9.2	0.8	1.8	7.7	0.6	0.9
n	27	27	27	27	43	27	43	43



Histogram of size distribution

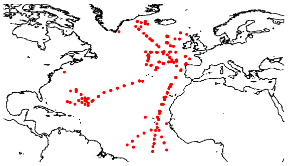


Variance explained: 98.9%
b0 = 0.046; b1 = 83.154

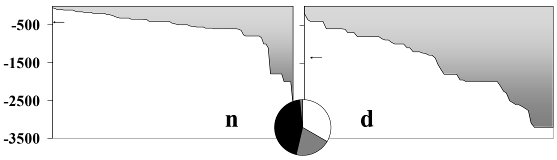
Remarks: horizontal hauls. The gear was used during the Bermuda Ocean Acre program along the IKMT 10' DDS (Gibbs & Karnella, 1987).

Engel Midwater Trawl (EMT 1600)

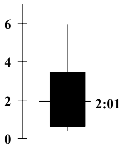
References: Krefft, 1974, 1976; Post, 1987, 1988; see also Stehmann, 1997. **Institutions:** Institut für Seefischerei (ISH), Hamburg, German. **R/Vessels:** Anton Dohrn = Walther Herwig I (AD = WHI) and Walther Herwig II (WH). **Programs (cruises): Bay of Biscay to Mar del Plata** (WHI-66-15; WHI-68-23); **Cape Town to Madeira** (WHI–71-36 2); **Overflow Expedition** (WH-73-51-2); **Denmark Strait to Lisbon** (WH-73-51 3); **GATE Expedition to Central Atlantic** (AD-74-176 58); **Sargasso Sea Expedition** (AD-79-210 2I); **Sargasso Sea to Bay of Biscay** (AD-79-210 2II); **Mid-Atlantic Ridge** (WH-82-52); **TIFI 8, W of Ireland** (WH-83-58); **Hatton Bank** (WH-86-76). **Data amount (n):** net hauls: **253**; records: **1751**; no specimens: **6208**; no species: **115. Data quality:** size: **30.1%**; depth: **98.0%**; time fishing: **95.6%**.



Geographical distribution



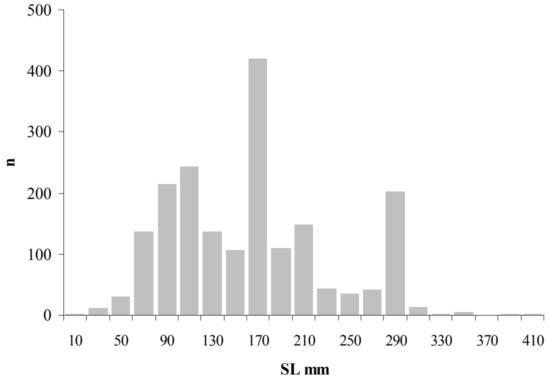
Depth profile. Night/ day net-hauls distribution



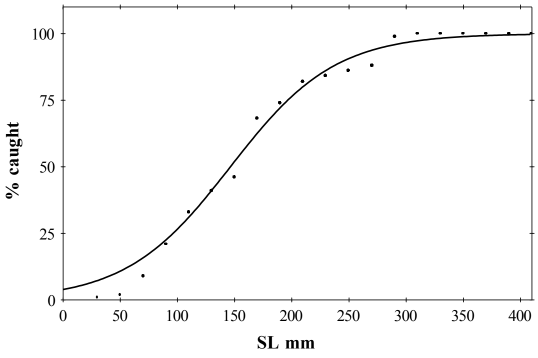
Time fishing

Standard haul basic statistics

EMT 1600	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	146.8	108.4	193.0	14.0	16.9	167.6	4.9	14.5
-95%	138.7	99.8	182.3	11.1	13.9	113.2	4.2	13.0
95%	154.9	117.0	203.8	16.9	19.9	221.9	5.6	15.9
min	42.0	11.5	42.0	0.1	0.2	0.2	0.2	1.0
max	415.0	415.0	415.0	230.6	163.1	4684.7	29.4	62.5
std dev	58.3	62.2	77.5	20.7	24.4	392.7	5.5	11.7
std err	4.1	4.4	5.4	1.5	1.5	27.6	0.3	0.7
n	203	203	203	203	259	203	256	256



Histogram of size distribution

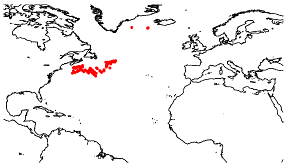


Variance explained: 97.9%;
b0 = 0.022; b1 = 146.312.

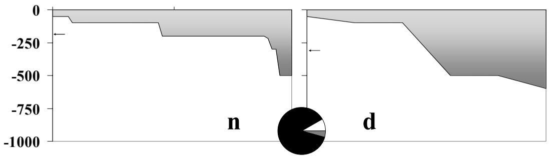
Remarks: The gear was used by the ISH during the large-scale programs on biogeography of Atlantic midwater fish. The trawl caught among the largest and heaviest stomiids, but failed to catch the smallest fish. Time fishing in the cruises report is given as the time while fishing at depth (Post, 1987). To estimate the time needed to shoot and recover the net, a relationship between pay out and pull in time against depth was calculated from hauls made during the "HE" 135 cruise (Table 2.1). A linear function (y = 3E-05x + 0.0016; R2 = 0.8974) indicates that the operation was slower during shallower hauls. Various fishing strategies were implemented between 1966 and 1986. The standard hauls fished horizontally; however, during the first programs the deeper hauls were oblique, with 3 steps of 10 min at different depth layers. This was necessary because the winch need to cool after about 2 hours of trawling.

Engel Midwater Trawl (EMT 80-630)

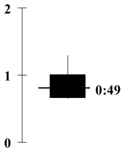
References: McKelvie, 1985a,b; McKelvie & Haedrich, 1985. **Institutions:** Department of Fisheries and Oceans (DFO), Canada; Institut für Seefischerei (ISH), Hamburg, German. **R/Vessels:** Belogorsk (BEL), Gadus Atlantica (GATL); Walther Herwig II (WH). **Programs (cruises): Cruises off Atlantic Canada** (BEL-79-02, BEL-79-03, BEL-79-04, BEL-79-05); **Other DFO Cruises** (GATL-81-051); **ISH Reykjanes Ridge Cruise** (WH-77). **Data amount (n):** net hauls: **98**; records: **173**; specimens: **584**; species: **28. Data quality (%):** size: **97.1**; depth: **94.9**; time fishing: **84.7**.



Geographical distribution



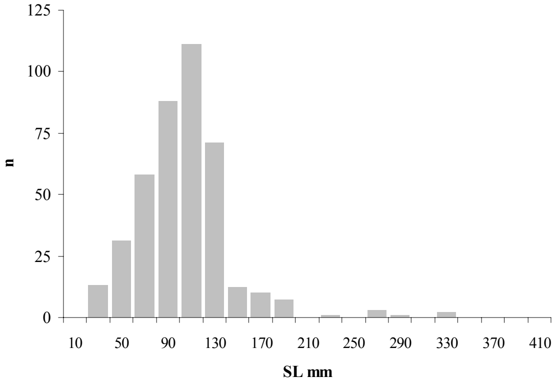
Depth profile. Night/ day net-hauls distribution



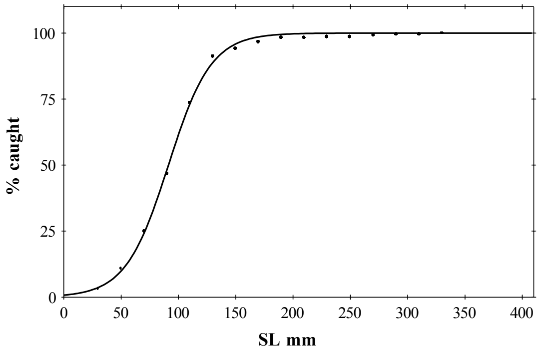
Time fishing

Standard haul basic statistics

EMT 80-630	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	101.4	79.4	126.4	3.7	5.2	17.7	2.0	3.2
-95%	92.7	71.3	114.3	1.4	3.9	7.7	1.8	2.2
95%	110.2	87.5	138.6	6.0	6.5	27.8	2.2	4.2
min	35.0	30.0	40.0	0.1	0.5	0.2	0.5	1.0
max	298.5	269.0	328.0	90.6	36.4	368.3	5.8	37.5
std dev	41.6	38.5	57.9	11.0	6.2	47.9	1.2	5.0
std err	4.4	4.1	6.1	1.2	0.6	5.1	0.1	0.5
n	89	89	89	89	92	89	92	92



Histogram of size distribution



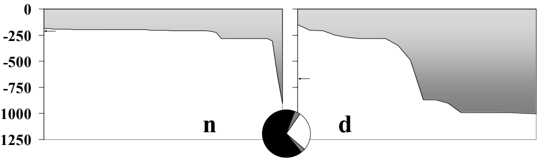
Variance explained: 98.98%;
b0 = 0.0535; b1 = 91.274

Remarks: The EMT 80-630 has a forenet mesh size larger than the previous EMT's. The gear was used by McKelvie to study the biogeography of the micronekton fish fauna off the Atlantic Canada. The net fished horizontally at depth.

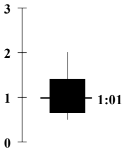
International Young Gadoid Pelagic Trawl (IYGPT 100)

References: Themelis, 1996; R. Haliday (pers. comm., 2000). **Institutions:** Department of Fisheries and Oceans (DFO), Canada; Dalhousie University, Halifax, Canada; Atlantic Reference Center (ARC), St. Andrews, Canada. **R/Vessels:** Alfred Needler (AN); Ekliptika (EK); Lady Hammond (LH). **Programs (cruises): Slope Sea Surveys** (EK-82-05; AN-83-011; LH-84-127; AN-86-057; AN-86-067; AN-87-089; AN-88-096; AN-88-110; AN-88-112; AN-89-119; AN-89-122; AN-89-126). **Data amount (n):** net hauls: **269**; records: **886**; specimens: **4325**; species: **48. Data quality (%):** size: **98.7**; depth: **98.5**; time fishing: **0**.

Geographical distribution



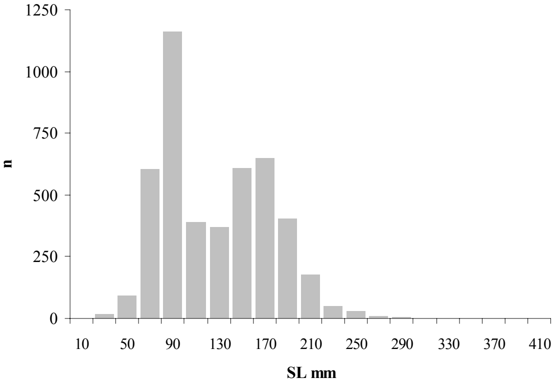
Depth profile. Night/ day net-hauls distribution



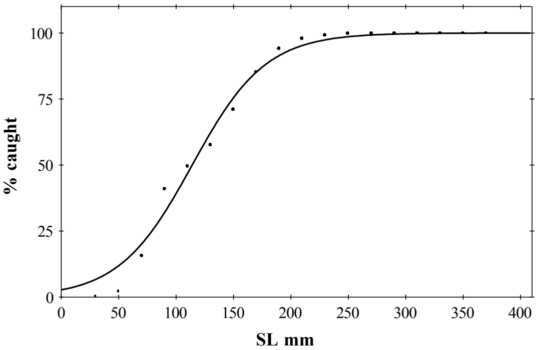
Time fishing

Standard haul basic statistics

IYGPT 100	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	115.9	70.4	175.3	4.8	15.1	83.9	3.2	3.8
-95%	111.4	66.8	167.2	4.1	13.7	67.4	3.0	3.5
95%	120.4	73.9	183.4	5.4	16.5	100.3	3.5	4.0
min	54.0	11.0	63.0	0.3	1.0	0.4	0.5	1.2
max	255.0	255.0	380.0	34.6	83.5	975.3	12.0	11.9
std dev	37.2	29.5	67.6	5.4	12.0	136.5	1.8	2.1
std err	2.3	1.8	4.1	0.3	0.7	8.3	0.1	0.1
n	268	268	268	268	269	268	268	268



Histogram of size distribution

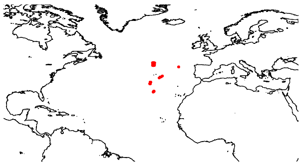


Variance explained: 98.22%;
b0 = 0.031; b1 = 114.005

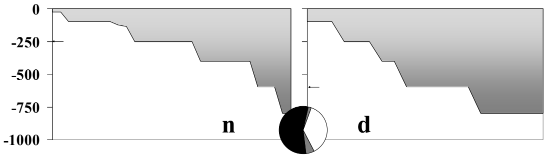
Remarks: The gear was used during a five year program to study the mesopelagic fish fauna in the Slope Water off Canada. Most of the data obtained don't include time haul length but Themelis (1996) reported a standard 30 min haul while fishing at depth (the exceptions were noted). Because time fishing in this study is the gap between net launch and net recovery, the time needed to launch and recover the net, a relationship was estimated from the operations made during the "Heincke"135 survey (Table 2.1), which used a similar net. The relationship was a linear function (see remarks under EMT 1600). The net fished horizontally while at depth. The IYGPT is being used by the Woods Hole Oceanographic Institution and NOAA to investigate the midwater fauna associated to Bear Seamount (New England Seamount Chain) (Moore et al., 2001, 2002, 2003b). The data from those cruises are not included in this study.

Young Fish Trawl (YFT 100)

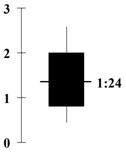
Institutions: Alfred Wegener Institution, (AWI), Bremerhaven, German. **R/Vessels:** Meteor (MET); Heincke (HE). **Programs (cruises):** **Meteor seamount** (MET-98-42-3); **Twins and Atlantis seamounts** (HE-2000-135). **Data amount (n):** net hauls: **54**; records: **196**; specimens: **555**; species: **34.** **Data quality (%):** size: **95.9**; depth: **100**; time fishing: **98.1**.



Geographical distribution



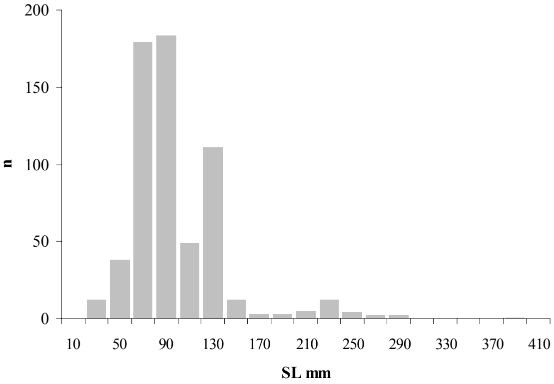
Depth profile. Night/ day net-hauls distribution



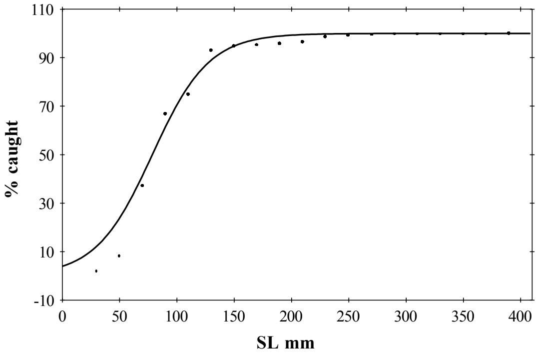
Time fishing

Standard haul basic statistics

YFT 100	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	96.5	59.2	156.7	2.9	7.4	24.0	2.7	5.1
-95%	88.8	53.2	135.6	2.2	5.2	15.3	2.0	4.1
95%	104.2	65.3	177.8	3.7	9.7	32.6	3.3	6.0
min	36.9	20.0	36.9	0.1	0.7	0.1	0.6	1.0
max	188.8	121.1	390.0	13.0	53.1	137.6	15.4	13.5
std dev	27.7	21.7	75.7	2.8	8.2	31.2	2.4	3.4
std err	3.8	3.0	10.5	0.4	1.1	4.3	0.3	0.5
N	52	52	52	52	54	52	53	53



Histogram of size distribution

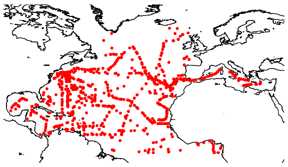


Variance explained: 95.59%;
b0 = 0.041; b1 = 8.539

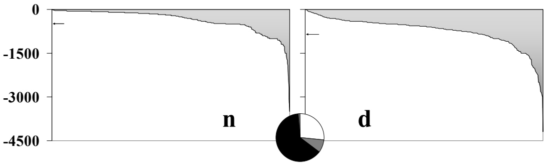
Remarks: The gear was used by the AWI to sample the micronekton associated with some Mid-Atlantic-Ridge seamounts. It fished at 5 depth layers to 800m, and at different distances from the seamounts summits (Pusch et al., 2002, 2004). Other programs carried out at Rockall Bank were not included in this study. The gear fished horizontally at depth. The programs undertaken around the Canary Islands (Bordes et al, 2000; Wienerroither, 2003) employed a commercial pelagic trawl probably similar to this young fish trawl.

Isaac-Kidd Midwater Trawl (IKMT 10')

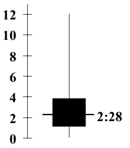
References: Backus & Craddock, 1977; Gibbs & Karnella, 1987; Kotthaus, 1972; Krueger et al., 1977; Post, 1987; Voss, 1967. **Institutions:** Woods Hole Oceanographic Institution (WHOI), USA; Institut für Seefischerei (ISH), Hamburg, German; National Oceanic and Atmospheric Administration (NOAA), USA; Institute of Marine Science, Miami, USA. **R/Vessels:** Academician Kurchatov (AK); Albatross IV (AL4); Anton Dohrn (AD); Argo (ARG); Atlantis (A); Atlantis II (AII); Blue Dolphin (BDOL); Chain (CH); Colombus Iselin (CI); Discovery (DISC); Frederik Hensen (FH); Gilliss (GLS); Gosnold (GSD); J.E. Pillsbury (PIL); Jean-Charcot (JCH); Knorr (KN); Meteor (MET); Oceanus (OC); Oregon II (ORII); Sands (SD); Trident (TR); Undaunted (UND); Walther Herwig (WH). **Programs: Atlantic Pelagic Zoogeography** (CH-61-17; CH-62-32; CH-63-35; AII-64-13; CH-65-49; AII-66-20; CH-66-60; CH-67-72; GSD-67-106; CH-68-85; AII-69-49; AII-70-59; KN-71-24; CH-72-105; AII-73-78; KN-74-38); **Other WHOI Cruises** (A-53-187; BDOL-53-8; A-54-196; A-54-202; A-55-219; CH-00-11; CH-62-25; CH-62-26; CH-66-60; AII-71-60; AII-72-71; AII-73-79; CH-73-110; CH-73-111; KN-73-35; AII-74-85; KN-75-53; KN-76-58; OC-76-11; AII-78-101); **Bermuda Ocean Acre** (TR-67-1; GLS-68-3; TR-68-4; SD-69-6; SD-70- 9; SD-71-11; SD-71- 12; SD-72- 13; SD-72- 14); **Gulf of Guinea Expedition** (PIL-64-1; PIL-65); **Noratlante** (JCH-69); **Canaries Basin Expedition** (MET-70); **Deepwater Dumpsite 106** (AL4-74-02; AL4-75-03; ORII-76); **Sargasso Sea Expedition** (AD-79; FH-79); **Other cruises** (AD-59:1; AK-73-14; AL4-69-07; CI-73-2; CI-74-06; DISC-59-1; DISC-61-1; DISC-65-SOND; GLS-73-1; GLS-73-2; Lusiad Expedition ARG-79; PIL-64-2; PIL-64-3; PIL-66-1; PIL-67-1; PIL-68-1; PIL-68-2; PIL-69-1; PIL-70-2; TR-65-23; TR-68-OA-5; TR-69-OA-8; TR-70-3; TR-70-4; TR-70-81; UND-66-03; WH-64-Z1). **Data amount (n):** net hauls: **1266**; records: **3721**; specimens: **12471**; species: **116. Data quality (%):** size: **65.2**; depth: **99.4**; time fishing: **94.5**.



Geographical distribution



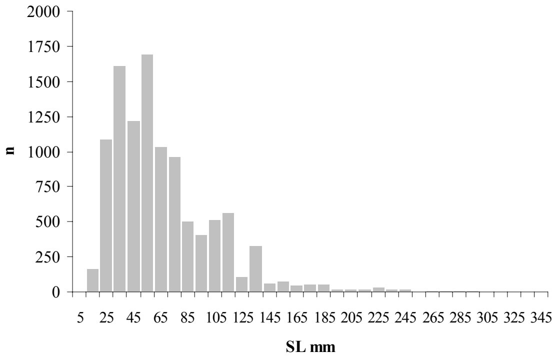
Depth profile. Night/ day net-hauls distribution



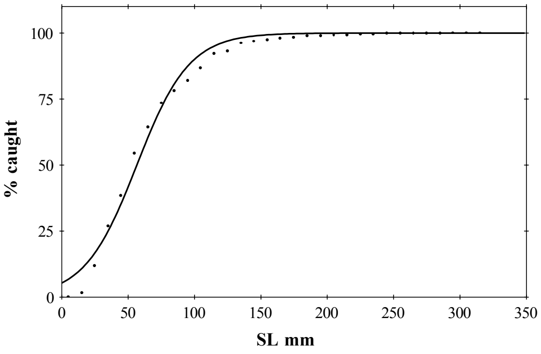
Time fishing

Standard haul basic statistics

IKMT 10'	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	71.1	46.8	106.0	2.1	4.7	7.6	1.4	5.2
-95%	68.6	44.4	102.2	1.7	4.0	4.9	1.3	4.8
95%	73.5	49.1	109.8	2.5	5.4	10.3	1.5	5.6
min	12.0	6.0	12.0	0.0	0.1	0.0	0.1	0.9
max	320.0	320.0	320.0	108.6	242.1	1059.8	30.0	60.0
std dev	39.8	38.7	61.8	6.4	12.2	44.5	1.8	7.7
std err	1.2	1.2	1.9	0.2	0.3	1.4	0.1	0.2
n	1022	1022	1022	1022	1266	1022	1242	1242



Histogram of size distribution

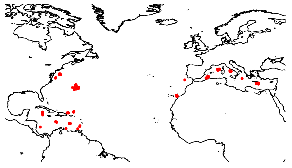


Variance explained: 98.61%;
b0 = 0.037; b1 = 45.624

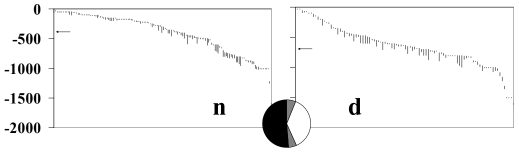
Remarks: The IKMT 10’ was the gear used by R. Backus and his team (WHOI) to sample the mesopelagial fauna under the scope of the Atlantic Pelagic Zoogeography program (Backus et al., 1965 1969, 1970; 1977; Backus & Craddock, 1977; among others). Since the 1960’s and until 1976 the net was widely adopted. It sampled almost throughout the North Atlantic basin, from the Gulf of Mexico to the Mediterranean, from the Greenland to the Gulf of Guinea. The first cruises (e.g. Backus et al., 1969) used a half-lined net. During the Atlantic Pelagic Zoogeography program the IKMT 10’ fished horizontally within the maximum intensity of the Deep Scattering Layer (DSL) to increase the catch. In general the IKMT 10’ was towed horizontally, but oblique and step hauls are also reported.

Isaac-Kidd Midwater Trawl (IKMT 10’ DDS)

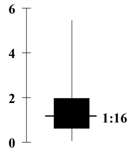
References: Foxton, 1969**;** Badcock, 1970; Gibbs & Karnella, 1987; Goodyear et al., 1972; Krueger et al., 1977; Bekker et al., 1975. **Institutions:** Institution of Oceanographic Science (IOS), Gormley, UK**;** Smithsonian Institution (USNM), Washington, USA; National Oceanic and Atmospheric Administration (NOAA), USA. **R/Vessels:** Discovery (DISC); Trident (TR); Sands (SD); Academician Kurchatov (AK); Albatross IV (AL4); Oregon II (ORII). **Programs: Sond Cruise** (DISC-65); **Bermuda Ocean Acre** (TR-68- 4; SD-69-6; SD-70-10; SD-71-11; SD-71-12; SD-72-13; SD-72-14); **Mediterranean Cruises** (TR-70-1-5); **Deepwater Dumpsite 106** (AL4-75-03; ORII-75; ORII-76); **Other Cruises** (AK-73-14). **Data amount (n):** net hauls: **335**; records: **613**; specimens: **962**; species: **69. Data quality (%):** size: **15.8**; depth: **100**; time fishing: **100**.



Geographical distribution



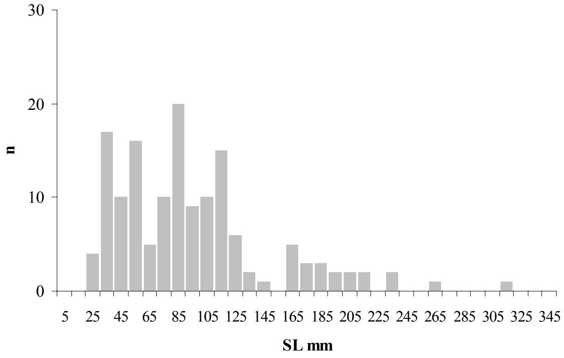
Depth profile. Night/ day net-hauls distribution



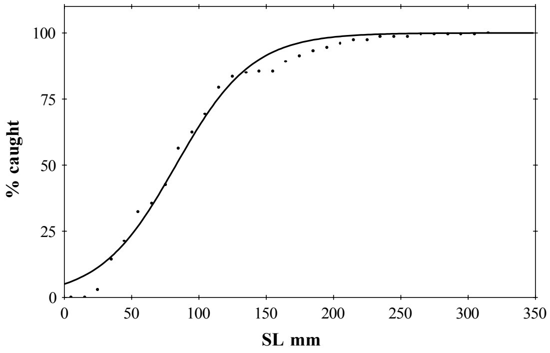
Time fishing

Standard haul basic statistics

IKMT 10’ DDS	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	91.9	81.1	104.8	4.8	2.6	10.9	1.7	7.6
-95%	80.6	70.1	90.0	2.7	2.3	5.2	1.5	6.5
95%	103.2	92.0	119.5	6.8	2.9	16.7	1.9	8.8
min	22.0	22.0	22.0	0.0	0.3	0.0	0.3	0.9
max	237.0	237.0	311.0	45.7	24.0	149.5	24.0	60.0
std dev	48.1	46.6	62.8	8.6	3.1	24.5	1.8	10.8
std err	5.7	5.5	7.4	1.0	0.2	2.9	0.1	0.6
n	72	72	72	72	335	72	327	327



Histogram of size distribution



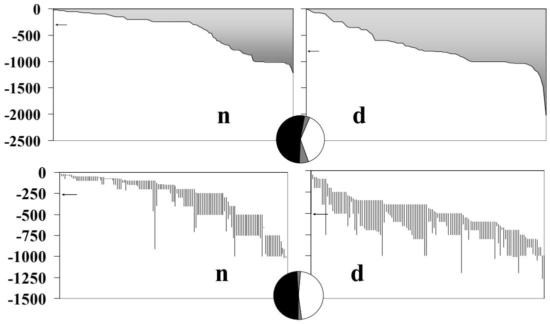
Variance explained: 98.80%;
b0 = 0.035; b1 = 82.896

Remarks: This gear is a standard IKMT 10' equipped with cod-end multi-closing devices to sample at discrete depth layers (DDS). The gear was widely used in both sides of the Atlantic. Catch data from some of those programs were obtained from published papers (Badcock, 1970; Bekker et al., 1975). The cod-end discrete depth samplers were reported to contaminate the catches, because fish can hang up on the net before to enter the cameras. The net fished horizontally within each depth layer.

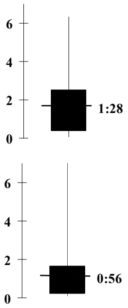
Multi Opening/ Closing Net and Environmental Sensing System MOCNESS 10 (MOC 10; MOC 10 N1)

References: Ring Group, 1981; Backus & Craddock, 1982 **Institutions:** Woods Hole Oceanographic Institution (WHOI). **R/Vessels:** Cape Hatteras (CHAT); Columbus Iselin (CI); Endeavor (EN); Knorr (KN); Oceanus (OC). **Programs:** KN-76-58 3; KN-76-62; EN-77-11; KN-77-65; KN-77-71; OC-78-49; OC-79-55; CHAT-92-1692; EN-92-238; CI-93-07; OC-93-225. **Data amount (n):** net hauls: **277**; records: **768**; specimens: **1781**; species: **62. Data quality (%)**: size: **88.8**; depth: **100**; time fishing: **97.8**. **Data amount N1 (n):** net hauls: **240**; records: **678**; specimens: **1665**; species: **61. Data quality (%):** size: **87.0**; depth: **95.8**; time fishing: **95.4**.

Geographical distribution



Depth profile. Night/ day net-hauls distribution

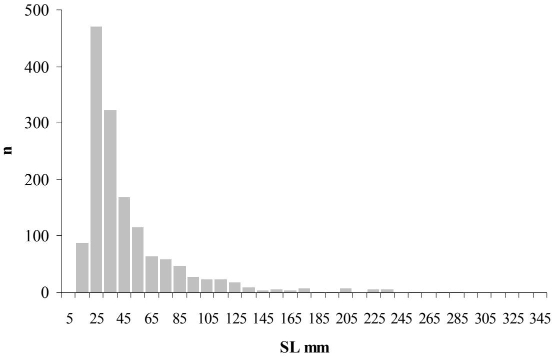


Time fishing

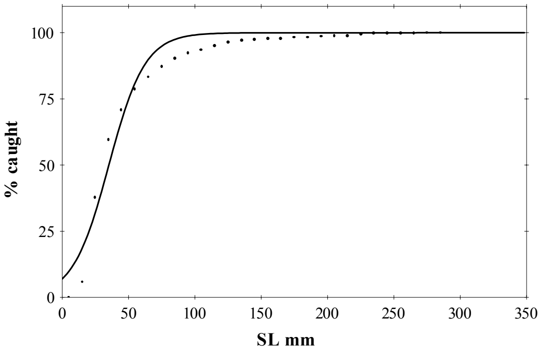
Standard haul basic statistics

MOC 10 N1	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	51.4	33.9	83.2	1.3	6.9	4.4	2.4	2.8
-95%	46.9	30.1	74.6	0.8	5.0	2.9	2.0	2.5
95%	55.9	37.8	91.8	1.7	8.8	5.9	2.8	3.1
min	16.0	9.0	16.0	0.0	0.3	0.0	0.3	0.9
max	255.5	224.0	287.0	23.9	163.5	71.0	40.0	11.7
std dev	33.2	28.1	63.3	3.4	14.9	10.8	3.1	2.0
std err	2.3	1.9	4.4	0.2	1.0	0.7	0.2	0.1
n	211	211	211	211	240	211	209	209

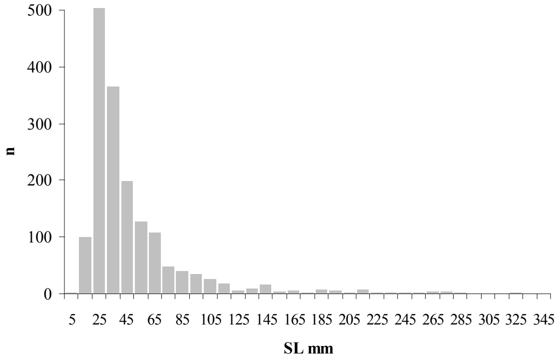
MOC 10	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	54.9	39.5	83.1	1.3	8.5	6.8	3.5	2.7
-95%	50.5	35.4	75.5	0.8	6.9	4.5	3.1	2.5
95%	59.3	43.5	90.7	1.7	10.2	9.1	3.8	3.0
min	13.0	4.0	13.0	0.0	0.1	0.0	0.1	0.9
max	223.0	223.0	322.0	38.3	148.6	177.8	20.5	12.6
std dev	35.7	33.3	61.7	3.5	13.7	18.9	2.9	2.1
std err	2.2	2.1	3.9	0.2	0.8	1.2	0.2	0.1
n	257	257	257	257	277	257	258	258



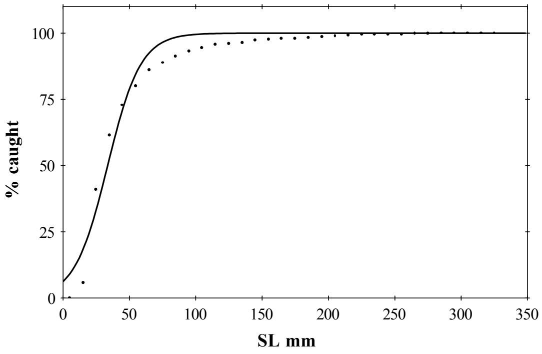
Histogram of size distribution



Variance explained: 96.4%;
b0 = 0.074; b1 = 35.198



Histogram of size distribution

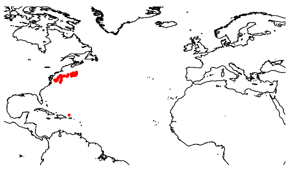


Variance explained: 96.57%;
b0 = 0.080; b1 = 33.592

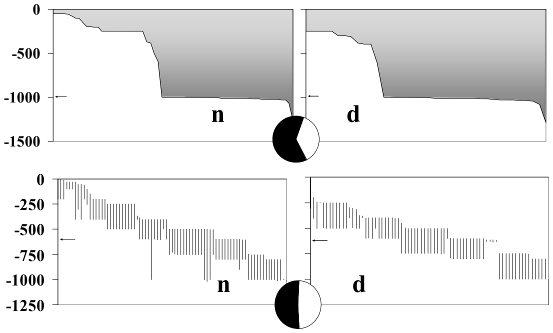
Remarks: The MOC 10 was used to study the oceanography of Gulf Stream cold-water rings advected into the Northern Sargasso sea (Ring Group, 1981). The sampling strategy (range of depth the discrete depth layers) varied between the cruises but in general the MOC 10 fished obliquely within layers of 200-300 m interval, down to 1200. The net 1 (MOC 10 N1) fished obliquely from the surface down to the deepest layer. Because Wiebe et al. (1985) demonstrated that it performed differently (i.e. towing angle and speed and volume of water filtered by unit time) the N1 hauls were analysed separately.

Multi Opening/ Closing Net and Environmental Sensing System MOCNESS 20 (MOC 20; MOC 20 N1)

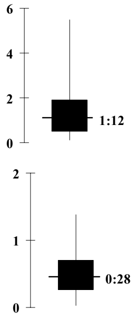
References: Craddock, et al., 1987, 1992. **Institutions:** Woods Hole Oceanographic Institution (WHOI), Woods Hole, USA. **R/Vessels:** Atlantis II (AII); Knorr (KN); Oceanus (OC). **Programs: Warm-Core Gulf Stream Rings Cruises** (AII-81-110; KN-82-98; OC-82-118; OC-82-121; OC-82-125); **Other Cruises** (KN-85-1). **Data amount (n):** net hauls: **153**; records: **456**; specimens: **2085**; species: **46. Data quality (%):** size: **99.3**; depth: **100**; time fishing: **100**. **Data amount N1 (n):** net hauls: **104**; records: **403**; specimens: **1229**; species: **36. Data quality (%):** size: **99.0**; depth: **100**; time fishing: **100**.



Geographical distribution



Depth profile. Night/ day net-hauls distribution

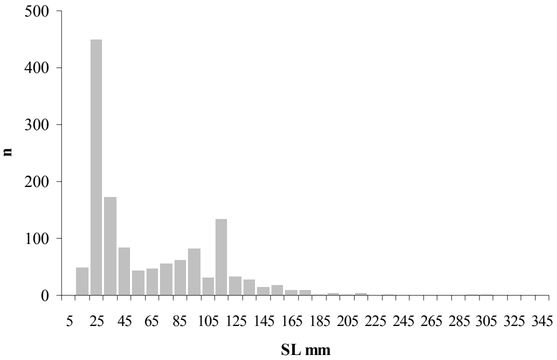


Time fishing

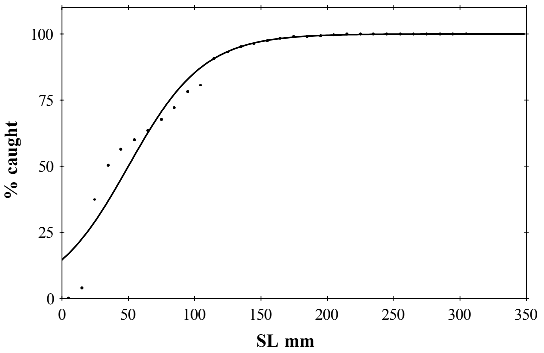
Standard haul basic statistics

MOC 20 N1	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	64.5	28.2	123.7	2.1	12.8	15.7	4.0	4.5
-95%	57.5	24.6	109.8	1.5	8.9	8.4	3.3	4.0
95%	71.5	31.7	137.6	2.7	16.7	23.0	4.6	5.0
min	11.0	11.0	11.0	0.0	0.4	0.0	0.2	0.9
max	165.0	131.0	303.0	15.3	140.0	352.4	20.0	12.5
std dev	35.9	18.2	71.5	3.2	20.1	37.5	3.4	2.4
std err	3.5	1.8	7.0	0.3	2.0	3.7	0.3	0.2
n	104	104	104	104	104	104	96	96

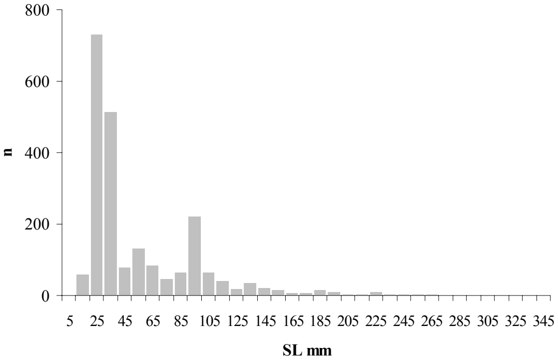
MOC 20	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	76.5	44.7	123.9	4.0	33.6	51.5	6.8	3.3
-95%	68.3	37.1	111.8	2.8	18.1	26.7	5.7	3.0
95%	84.8	52.3	136.1	5.1	49.0	76.4	7.9	3.7
min	17.0	13.0	17.0	0.0	1.3	0.0	1.1	1.2
max	275.0	275.0	290.0	45.4	700.0	1754.0	70.0	11.9
std dev	51.4	47.6	75.9	7.3	96.8	155.4	7.0	2.2
std err	4.2	3.8	6.1	0.6	7.8	12.6	0.6	0.2
n	153	153	153	153	153	153	150	150



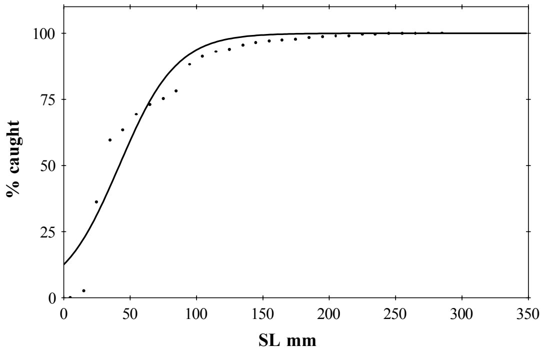
Histogram of size distribution



Variance explained: 95.10%;
b0 = 0.035; b1 = 50.073



Histogram of size distribution

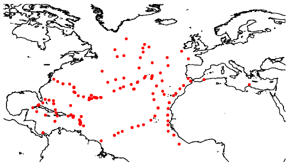


Variance explained: 93.73%;
b0 = 0.046; b1 = 41.792

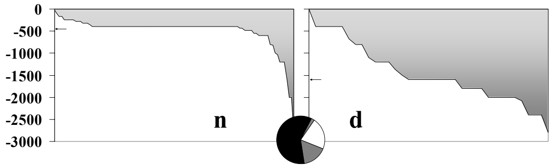
Remarks: The MOCNESS 20 is probably the most sophisticated micronekton trawl. It is a large multi-net gear equipped with fine mesh nets and sophisticated electronics. Craddock et al. (1987, 1992) used this gear to study the meso-scale variability associated to warm-core-rings, off Canada. The net 1 (MOC 20 N1) fished open from the surface down to the deepest layer. Because Wiebe et al. (1985) demonstrated that it performed differently (i.e. towing angle and speed and volume of water filtered by unit time) the N2 hauls were grouped separately. In general, the MOC 20 was fished obliquely within discrete depth layers of 250, 200 and 150m (from deeper to shallower hauls).

Ring net 3m (R 3m)

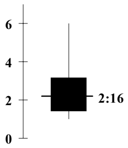
References: Murray & Hjort, 1912; Schmidt, 1929; Anon., 1934; Tåning, 1944; Grey, 1955. **Institutions:** University of Bergen, Norway; Danish Commission for Investigation of the Sea, Carlsberg Foundation, Dana Committee, Denmark. **R/Vessels:** Dana II (DII); Caryn (CRN); Michael Sars (MCHS). **Programs (cruises): North Atlantic Deep Sea Expedition** (MCHS-10); **III Dana Expedition** (DII-21-22); **Expedition Round the World** (DII, 28-30); CRN-48. **Data amount (n):** net hauls: **174**; records: **352**; specimens: **541**; species: **60. Data quality (%):** size: **75.6**; depth: **99.4**; time fishing: **88.5**.



Geographical distribution



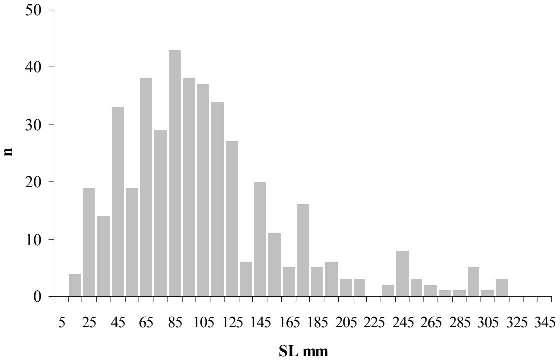
Depth profile. Night/ day net-hauls distribution



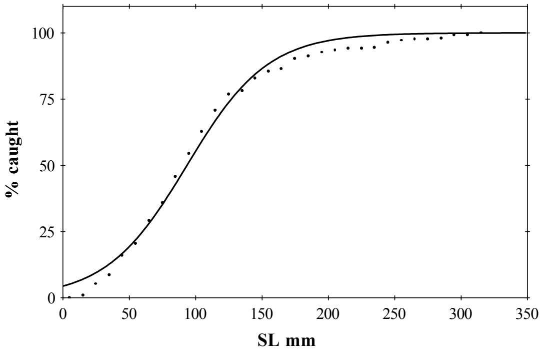
Time fishing

Standard haul basic statistics

R 3m	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
Mean	112.3	89.3	139.6	6.1	1.4	7.6	0.9	2.8
-95%	102.7	79.2	127.3	4.1	1.2	5.4	0.8	2.4
95%	121.9	99.3	151.9	8.1	1.6	9.8	1.0	3.3
Min	25.0	20.0	25.0	0.0	0.3	0.0	0.3	0.9
Max	320.0	320.0	320.0	108.6	7.7	79.9	5.0	20.0
std dev	59.2	61.9	75.7	12.4	1.3	13.7	0.6	3.1
std err	4.8	5.1	6.2	1.0	0.1	1.1	0.0	0.2
n	149	149	149	149	174	149	173	173



Histogram of size distribution

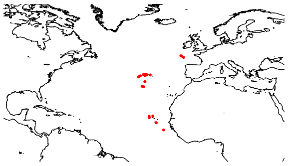


Variance explained: 99.09%;
b0 = 0.0329; b1 = 93.433

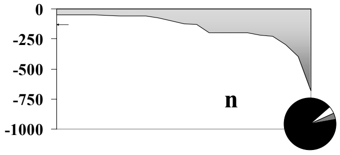
Remarks: This ring net was used mainly in a vertical array along with other ring nets (i.e. R1m, R1.5m and R2m). Normally the E300 (DANA terminology) was fixed to the extremity of the towing cable, and then 4 to 5 smaller ring nets were attach at regular intervals to the towing cable. Several net-hauls were taken at the same haul. The R3m was also called a "young fish trawl" because it has a very large mesh size. The gear fished horizontally or obliquely.

Rectangular Midwater Trawl (RMT 8)

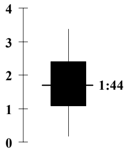
Institutions: Department of Oceanography and Fisheries, University of the Azores; Institute of Oceanographic Sciences (IOS), Wormley, UK. **R/Vessels:** Arquipélago (ARQ); Frederick Russel (FRR) **Programs (cruises): Azores front dynamic** (ARQ-97-FCA); **ARICTIO I** (ARQ-99-ARI); other cruises (FRR-82)*. **Data amount (n) *:** net hauls: **29**; records: **58 (89*)**; specimens: **142 (920*)**; species: **21 (8 *). Data quality (%):** size: **91.4**; depth: **96.6**; time fishing: **79.3.**



Geographical distribution



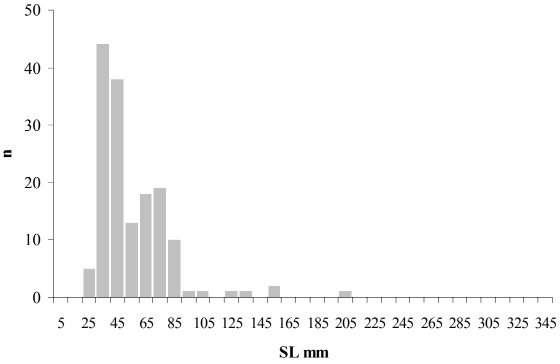
Depth profile. Night/ day net-hauls distribution



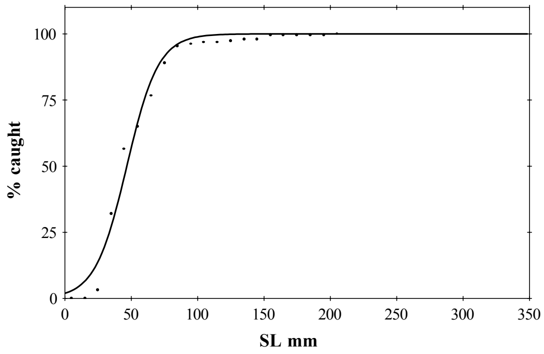
Time fishing

Standard haul basic statistics

RMT 8	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	58.5	44.9	79.8	0.8	3.9	1.6	1.9	2.7
-95%	49.1	35.6	62.6	0.2	1.1	0.7	0.7	2.1
95%	67.9	54.2	97.0	1.3	6.7	2.4	3.1	3.2
min	22.0	22.0	22.0	0.0	0.3	0.1	0.3	1.0
max	122.0	122.0	201.0	5.9	36.0	9.5	16.0	5.4
std dev	22.8	22.6	41.6	1.4	7.4	2.1	3.1	1.4
std err	4.6	4.5	8.3	0.3	1.4	0.4	0.6	0.3
n	25	25	25	25	29	25	26	26



Histogram of size distribution

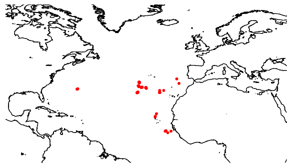


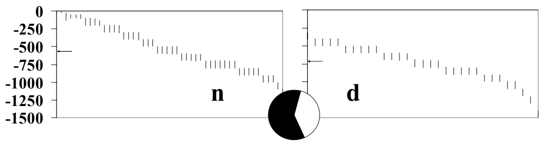
Variance explained: 98.59%;
b0 = 0.084; b1 = 46.621

Remarks: The open version of the RMT 8 was seldom used by the IOS. The material referred to this gear came mainly from midwater surveys made around the Azores by the author. The choice of an open RMT 8 was imposed by the size of the research vessels available. Several stations were made at the proximity of a seamount (Princess Alice Bank). * The cruise made on the R/V "Frederick Russel" in 1982 at the Biscay Bay aimed for study the influence of electric light on the capture of deep-sea fish (Swinney et al., 1986; Clarke & Pascoe, 1985) (see also RMT 10 and RMT 50). Swinney et al. (1986) listed the fish caught but does not give any cruise data.

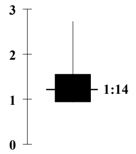
Rectangular Midwater Trawl (opening-closing system) (RMT 8 MC)

References: Badcock and Merret (1976); Angel, 1989; Hargreaves, 1990. **Institutions:** Institution of Oceanographic Science (IOS), Wormley, UK. **R/Vessels:** Discovery (DISC). **Programs (cruises):** DISC-72; DISC-73; DISC-81-120; DISC-81-121; more 16 scattered hauls. **Data amount (n):** net hauls: **119**; records: **315**; specimens: **1116**; species: **51. Data quality (%):** size: **80.6**; depth: **96.6**; time fishing: **80.5**.


Geographical distribution



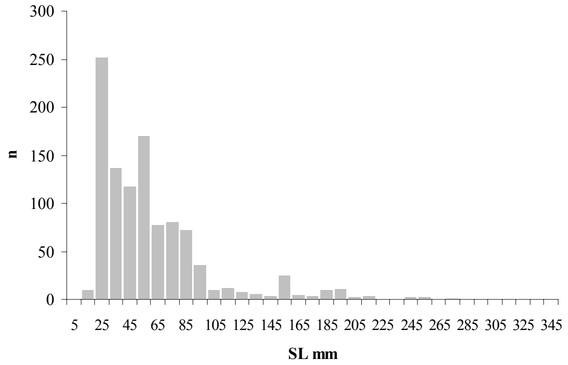
Depth profile. Night/ day net-hauls distribution



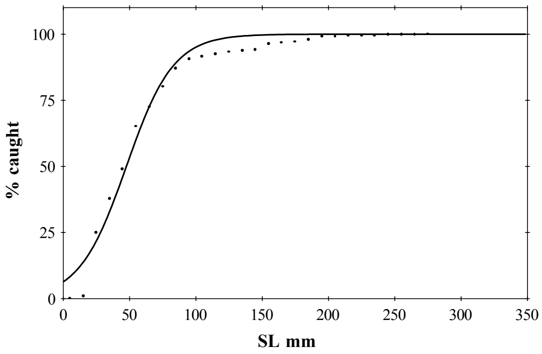
Time fishing

Standard haul basic statistics

RMT 8 MC	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	69,1	45,7	109,3	1,7	7,8	7,6	2,2	2,7
-95%	61,0	37,7	95,6	1,0	6,1	5,6	1,9	2,3
95%	77,2	53,7	123,1	2,4	9,5	9,5	2,6	3,1
min	19,0	15,0	19,0	0,0	0,6	0,0	0,4	1,0
max	200,0	200,0	280,0	26,3	48,3	46,6	11,0	10,7
std dev	40,2	39,8	68,4	3,5	9,4	9,8	1,9	2,2
std err	4,1	4,0	6,9	0,4	0,9	1,0	0,2	0,2
n	97	97	97	97	118	97	111	111



Histogram of size distribution

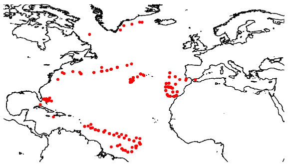


Variance explained: 97,9%;
b0 = 0,056; b1 = 47,554

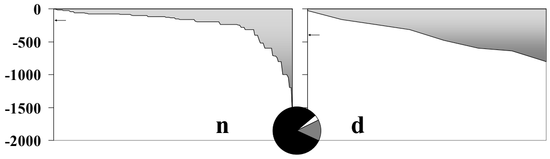
Remarks: The first RMT 8 version had only one open-closing net. Then the system accommodated 3 nets. Later the IOS built the RMT 1+8, a multi-net device with two frames (1 and 8 m^2) to sample simultaneously meso- and macrozooplankton and micronekton. Most of the midwater fish sampled by the IOS programs was not incorporated into the Stomiidae database (see BMNH entry in Appendix B). Other programs used the multi-net RMT 8 (e.g. the Amsterdam Mid North Atlantic Plankton Expedition; van der Spoel, 1981, 1985; van der Spoel & Meerding, 1983), but that data also was not available for this study. The data used here were compiled from Badcock and Merret (1976) and from samples caught at the Azores Front region (Domansky, 1986; Angel, 1989) and studied at the BMNH. Some material caught off Bermuda was deposited in the USNM. The sampling strategy adopted by the IOS was standardized and the water column was evenly sample at horizons of 50 to 100m down to 1200 m.

Rectangular Midwater Trawl (RMT 10)

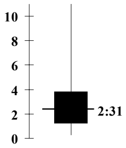
Institutions: Woods Hole Oceanographic Institution (WHOI), USA; Institution of Oceanographic Science (IOS), Wormley, UK. **R/Vessels:** Cape Florida (CFL); Challenger (CHG); Columbus Iselin (CI); Corwith Cramer (CC); Endeavor (EN); Knorr (KN); Oceanus (OC). **Programs (cruises): WHOI Cruises** (OC-77-22; KN-82-94; OC-84-158; OC-86-176; OC-87-183); **Madeira Cruise** (CHG-83-14); **Other Cruises** (CI-83-7; CI-83-11; CFL-84-13; EN-85-133; CC-90-110). **Data amount (n):** net hauls: **238**; records: **914**; specimens: **2107**; species: **79. Data quality (%):** size: **60.4**; depth: **98.7**; time fishing: **97.5**.



Geographical distribution



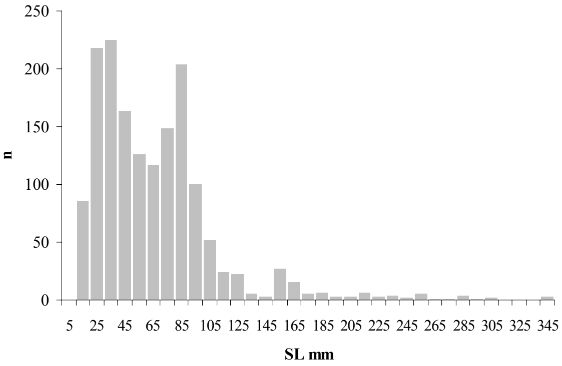
Depth profile. Night/ day net-hauls distribution



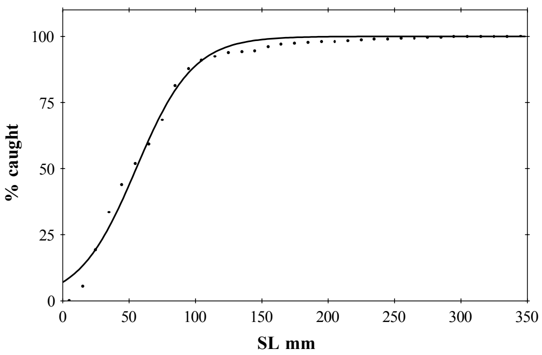
Time fishing

Standard haul basic statistics

RMT 10	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	69.2	41.5	110.7	1.7	4.4	5.8	1.5	5.1
-95%	62.9	35.7	99.9	1.1	3.5	4.0	1.3	4.3
95%	75.5	47.3	121.5	2.3	5.3	7.6	1.7	5.9
min	18.0	10.0	18.0	0.0	0.2	0.0	0.2	0.9
max	270.0	270.0	345.0	27.0	76.0	85.0	7.2	60.0
std dev	41.2	38.2	71.1	3.7	7.1	11.9	1.2	6.0
std err	3.2	2.9	5.5	0.3	0.5	0.9	0.1	0.4
n	169	169	169	169	238	169	195	195



Histogram of size distribution

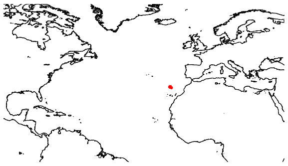


Variance explained: 98.93%;
b0 = 0.045; b1 = 55.289

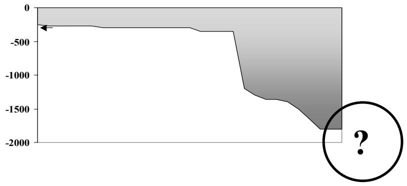
Remarks: The non-closing RMT 10 was used by the WHOI to replace the IKMT 10' to sample along geographical transects. Clarke and Pascoe (1985) used the gear (alongside the RMT 50) to test the influence of light on the captures of micronekton. The data from the two parties were pooled.

Rectangular Midwater Trawl (RMT 50)

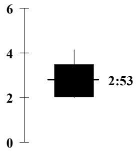
References: Clarke & Pascoe, 1985**. Institutions:** Institution of Oceanographic Science (IOS), Wormley, UK. **R/Vessels:** Challenger (CHG). **Programs (regional cruises): Madeira Cruise** (CHG-83-14). **Data amount (n):** net hauls: **30**; records: **303**; specimens: **1557**; species: **42. Data quality (%):** size: **84.1**; depth: **96.7**; time fishing: **0.**



Geographical distribution



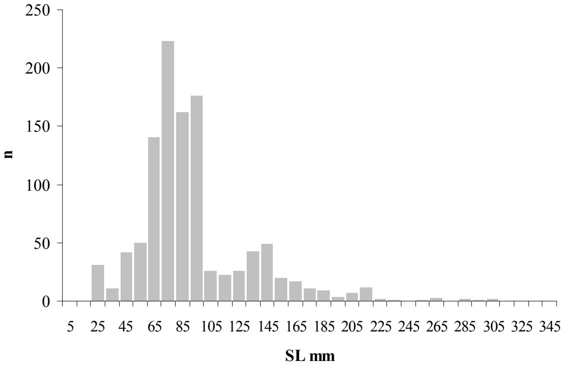
Depth profile. Night/ day net-hauls distribution



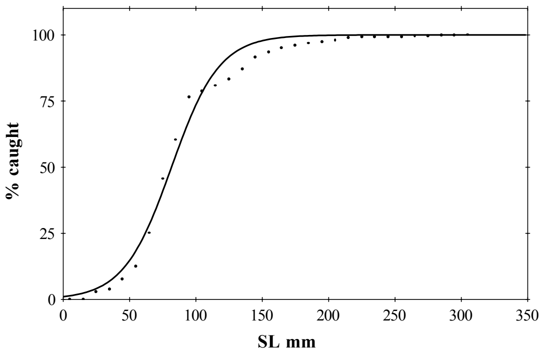
Time fishing

Standard haul basic statistics

RMT 50	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	89.9	33.1	217.2	3.3	19.4	68.6	3.5	12.2
-95%	84.7	29.7	193.3	2.4	14.8	40.5	3.1	10.8
95%	95.2	36.6	241.0	4.3	24.0	96.7	4.0	13.6
min	52.0	22.0	56.0	0.4	0.7	0.3	0.4	1.3
max	116.1	55.0	335.0	10.8	48.2	307.1	7.2	21.1
std dev	14.0	9.2	63.8	2.6	12.3	75.3	1.2	3.8
std err	2.5	1.7	11.7	0.5	2.3	13.7	0.2	0.7
n	30	30	30	30	30	30	30	30



Histogram of size distribution

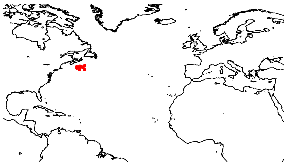


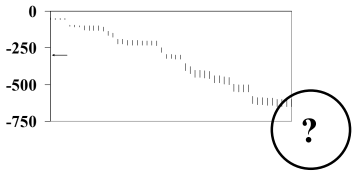
Variance explained: 98.85%;
b0 = 0.056; b1 = 81.565

Remarks: Clarke & Pascoe (1985) used the RMT 50 during the cruise 14th of "Challenger" off Madeira, to test the effect of artificial light on the catch volumes and body size of mesopelagic micronektonic fauna (see also Swinney et al., 1986 and Clarke & Pascoe, 1998). The authors concluded that, for the majority of the species, a 70 watt light enhanced significantly the captures in numbers of individuals and in biomass. Moreover, they concluded that the fish caught were larger and heavier than to those caught without lights. The data about the period of the day the hauls were made were not available.

Tucker trawl - TT 5

References: Themelis, 1996; R. Haliday (pers. comm.). **Institutions:** Department of Fisheries and Oceans (DFO), Canada; Dalhousie University, Halifax, Canada; Atlantic Reference Center (ARC), St. Andrews, Canada. **R/Vessels:** Alfred Needler (AN). **Programs (regional cruises):** Slope Sea Surveys (AN-88-096; AN-88-112; AN-89-119; AN-89-122; AN-89-126). **Data amount (n):** net hauls: **51**; records: **121**; specimens: **649**; species: **16.** **Data quality (%):** size: **100**; depth: **100**; time fishing: **0**





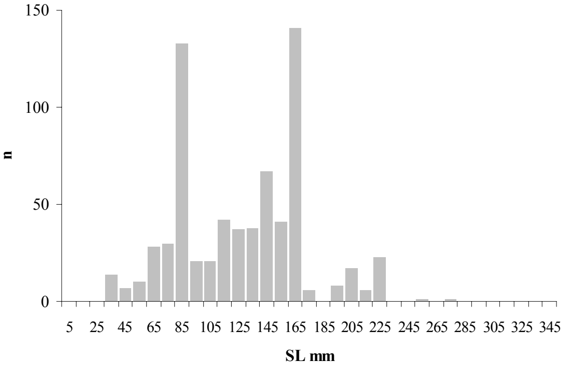
Geographical distribution

Depth profile. Night/ day net-hauls distribution

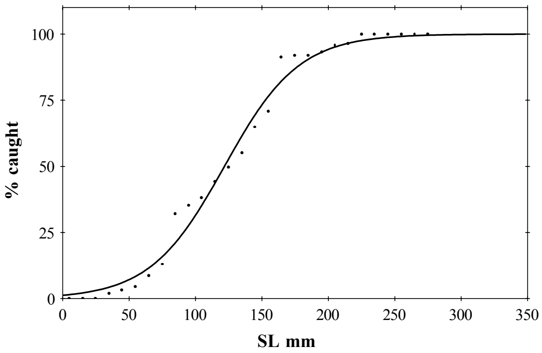
Time fishing

Standard haul basic statistics

TT 5	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
Mean	104.8	67.8	150.6	3.8	25.5	192.0	4.5	2.7
-95%	93.9	61.7	130.3	2.5	17.3	72.1	3.8	2.3
95%	115.7	74.0	171.0	5.0	33.6	311.9	5.3	3.1
Min	39.5	24.0	41.0	0.1	2.0	0.3	2.0	1.2
Max	192.1	130.0	290.0	17.7	124.0	2199.3	14.0	8.3
std dev	38.7	21.9	72.4	4.4	28.8	426.3	2.5	1.5
std err	5.4	3.1	10.1	0.6	4.0	59.7	0.4	0.2
N	51	51	51	51	51	51	51	51



Histogram of size distribution

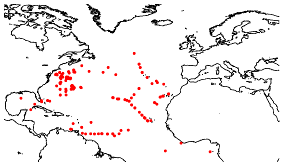


Variance explained: 98.93%;
b0 = 0.036; b1 = 121.725

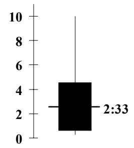
Remarks: The Tucker trawl was used to study the vertical structure and dynamic of Slope Water mesopelagic fish fauna. Fishing time was not available but Themelis (1996) refers 30 min for a standard net-haul. Two versions of TT were extensively used by University of South Florida (USF) in the Gulf of Mexico (e.g. Hopkins & Lancraft, 1984, Sutton & Hopkins, 1996a). However, only a small and inaccurate fraction of that data is available for this study (e.g. R/V Suncoaster 85-1, 85-03 and 85-12). The data associated with TT 5 should be reviewed and the addition of the material from the USF would improve the accuracy of the analysis.

Neuston net (nn)

References: Backus & Craddock, 1977; Gibbs & Karnella, 1987; Krueger et al., 1977; **Institutions:** Woods Hole Oceanographic Institution (WHOI), Woods Hole, USA; National Oceanic and Atmospheric Administration (NOAA), USA; Institute of Marine Science, Miami, USA; **R/Vessels:** Albatross IV (AL4); Argus (AR); Atlantis II (AII); Chain (CH); Columbus Iselin (CI); Delaware (DL); Gerda (GRD); Gilliss (GLS); Gosnold (GSD); Hudson (HD); Knorr (KN); Oregon II (ORII); Pillsbury (PIL); Sands (SD); **Programs (regional cruises): Atlantic Pelagic Zoogeography** (AII-64-13; CH-65-49; AII-66-20; CH-66-60; CH-67-72; CH-67-75; CH-68-85; GSD-68-132; AII-69-49; AII-70-59; AII-71-60; CH-72-105; AII-73-78; KN-74-38); **Other WHOI cruises** (AII-73-79; KN-77-71; AII-81-110); **Bermuda Ocean Acre** (GLS-68-3; SD-70-10; SD-71- 12; SD-72- 13; SD-72- 14); **Deepwater Dumpsite 106** (AL4-75-03; ORII-75); **Other cruises (**AL4-69-07; AR-80-03; CI-83-11; DL-57-1; DL-57-2; DL-58-1; DL-60-06; GLS-82-1; GRD-63-2; HD-65-BIO3; KN-76-58 2; PIL-64-1; **Data amount (n):** net hauls: **200**; records: **227**; specimens: **1370**; species: **11; Data quality (%):** size: **75,8**; depth: **100**; time fishing: **90,0;**



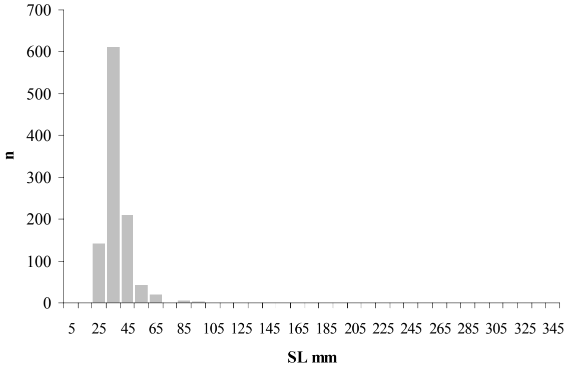
Geographical distribution



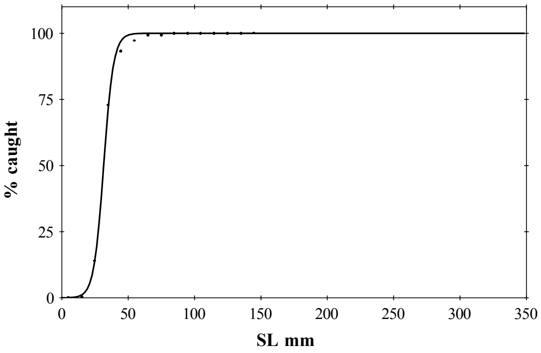
Time fishing

Standard haul basic statistics

nn	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
Mean	38.1	32.8	43.6	0.5	3.5	1.3	0.9	1.3
-95%	35.9	30.6	41.1	0.4	2.8	0.9	0.8	1.3
95%	40.3	35.0	46.0	0.6	4.2	1.7	1.1	1.4
Min	19.0	19.0	19.0	0.0	0.2	0.0	0.1	0.9
Max	141.0	141.0	141.0	4.4	29.0	25.7	4.0	2.8
std dev	13.5	13.9	15.5	0.6	4.8	2.6	1.0	0.5
std err	1.1	1.1	1.3	0.1	0.3	0.2	0.1	0.0
N	152	152	152	152	197	152	195	195



Histogram of size distribution



Variance explained: 99.86%;
b0 = 0.270; b1 = 31.546

Remarks: The sampler was fished at the surface (half-submerged) and caught stomiids only during night time. The net was towed at surface as the ship was steaming at less than 4 knots even while trawling other nets. Only two stomiid species were recurrently sampled at the most shallower epipelagic layer of the North Atlantic.

Isaacs-Kidd Midwater Trawl - IKMT 6'

References: Gibbs & Karnella, 1987. **Institutions:** University of Miami Marine Laboratory (UMML) and National Marine Fisheries Service, at Miami and Pascagoula Florida, USA**; R/Vessels:** Atlantis (A); Gerda (GRD); Trident (TR). **Programs (regional cruises):** A-62-286; GRD-62; GRD-63; GRD-64; GRD-64; GRD-65. Ocean Acre Program: TR-67-1; TR-68-2. **Data amount (n):** net hauls: **78**; records: **135**; specimens: **185**; species: **42**. **Data quality (%):** size: **53.3**; depth: **96.2**; time fishing: **69.2**.

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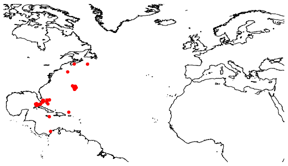
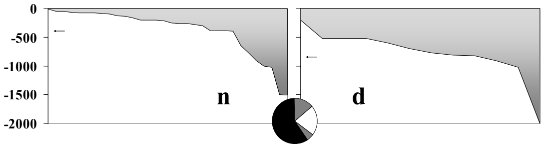
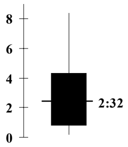


Geographical distribution



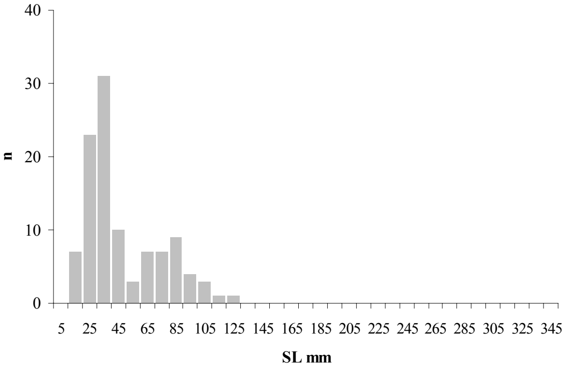
Depth profile. Night/ day net-hauls distribution



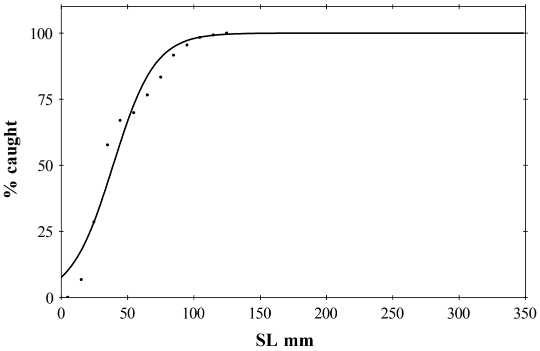
Time fishing

Standard haul basic statistics

IKMT 6'	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	50.2	45.6	55.4	0.6	1.8	0.5	1.2	1.4
-95%	42.7	37.7	47.4	0.3	0.9	0.3	0.6	1.3
95%	57.8	53.6	63.5	0.8	2.7	0.8	1.7	1.6
min	17.0	16.0	17.0	0.0	0.2	0.0	0.2	0.9
max	124.0	124.0	124.0	6.2	24.0	4.8	18.0	4.9
std dev	28.3	29.7	30.0	1.0	4.0	0.9	2.5	0.8
std err	3.8	4.0	4.0	0.1	0.5	0.1	0.3	0.1
n	56	56	56	56	78	56	74	74



Histogram of size distribution

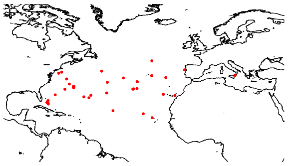


Variance explained: 95.68%;
b0 = 0.0635; b1 = 39.085

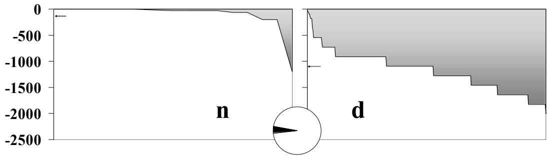
Remarks: The gear was rarely used the North Atlantic. Conversely, it was largely adopted in many studies made at the Pacific (e.g. Aron et al., 1964; Atsatt & Seapy, 1974). The open version of the IKMT 6' was used mainly by the UMML. The gear was used (with and without a discrete depth sampler) during the first two Ocean Acre cruises (TR-67-1; TR-68-2; Gibbs & Karnella, 1987); but then it was replaced by the larger IKMT 10' DDS.

Ring net – R1m

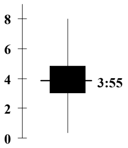
References: Murray & Hjort, 1912; Schmidt, 1929; Beebe, 1932a,b; Anon, 1934. **Institutions:** University of Bergen, Norway; Danish Commission for Investigation of the Sea; Carlsberg Foundation; Dana Committee, Denmark; New York Zoological Society (NYZS), USA. **R/Vessels:** Crawford (CR); Dana II (DII); Gladisfen (GLF); Margrethe (MARG); Michael Sars (MCHS); Pillsbury (PIL); Undaunted (UND); Wheeler (WHL). **Programs (cruises): NYZS Bermuda Oceanographic Expedition** (GLF, 29-31, 34); **Other cruises: North Atlantic Deep Sea Expedition** (MCHS-10); **III Dana Expedition** (DII, 21-22); and CR-62-66; DII-31-1; MARG-13-1; ONR-TOTO-62; PIL-64-3; UND-66-03; WHL-28-35). **Data amount (n):** net hauls: **678**; records: **1058**; specimens: **1379**; species: **49. Data quality (%):** size: **26.8**; depth: **100**; time fishing: **95.0**.



Geographical distribution



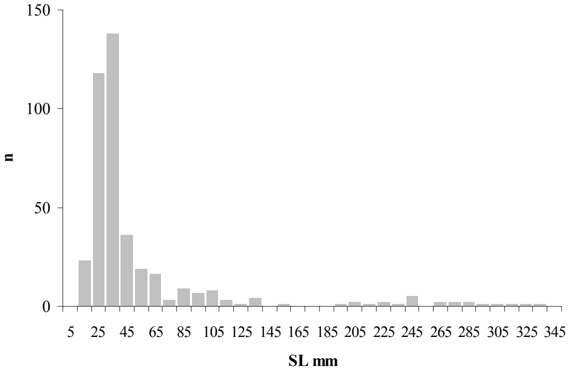
Depth profile. Night/ day net-hauls distribution



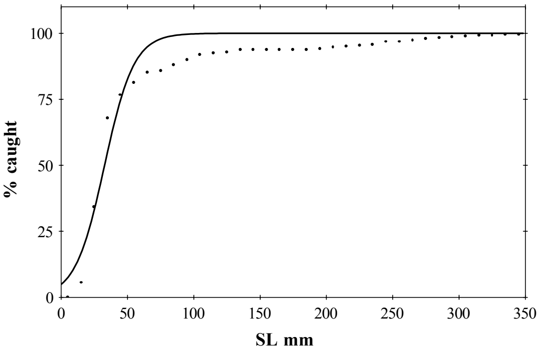
Time fishing

Standard haul basic statistics

R 1m	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	64.1	61.0	67.2	5.9	0.5	3.1	0.4	1.6
-95%	55.5	52.4	58.2	3.4	0.5	1.6	0.4	1.5
95%	72.8	69.6	76.1	8.3	0.6	4.6	0.4	1.7
min	13.0	12.0	13.0	0.0	0.1	0.0	0.1	0.9
max	333.0	333.0	355.0	122.4	6.0	103.1	6.0	20.0
std dev	69.1	68.6	71.4	19.5	0.5	12.0	0.3	1.3
std err	4.4	4.4	4.5	1.2	0.0	0.8	0.0	0.1
n	246	247	247	247	678	247	650	650



Histogram of size distribution

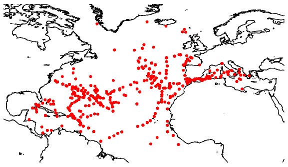


Variance explained: 92,71%;
b0 = 0,090; b1 = 32,732

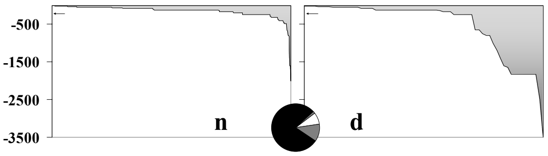
Remarks: the R1m was the standard gear used by W. Beebe during the Bermuda Oceanographic Expedition. Several nets were attached to the towing cable and each tow produced various samples from different depths. Other programs used the R1m but not as the standard gear to catch micronekton. The data from other cruises represents only 6% of the R1m net-hauls.

Ring net - R2m

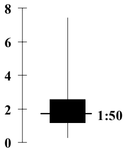
References: Schmidt, 1929; Anon, 1934; Tåning, 1944; Grey, 1955. **Institutions:** Danish Commission for Investigation of the Sea; Carlsberg Foundation; Dana Committee, Denmark; New York Zoological Society (NYZS), USA. **R/Vessels:** Atlantis (A); Caryn (CRN); Dana (D); Dana II (DII); Gerda (GRD); Gladisfen (GLF); Ingolf (ING); Margrethe (MARG); Pagan (PAG); Rosaura (ROS); St. Thomas (STT); Thor (THOR); Undaunted (UND). **Programs: I, II and III Dana Expeditions** (D, 20; DII, 21; DII, 21-22); **Expedition Round the World** (DII, 28-30); **Other Danish Expeditions** (THOR-04-1; THOR-04-2; THOR-04-3; THOR-05-1; THOR-05-2; THOR-06-1; THOR-08-1; THOR-09-1; THOR-10-1; ING-11-1; ING-12-1; ING-12-2; MARG-13-1; DII-31-1; DII-47-1); **NYZS Bermuda Oceanographic Expedition** (GLF, 1929-31); **Other cruises** (A-31-Z3; A-32-1; CRN-48-1; GRD-58-1; Harvard-Havana Expedition; PAG-13-1; ROS-37-1; ROS-37-2; STT-12-1; STT-12-2; UND-66-03. **Data amount (n):** net hauls: **904**; records: **1718**; specimens: **4760**; species: **97. Data quality (%):** size: **87.4**; depth: **98.9**; time fishing: **90.9**.



Geographical distribution



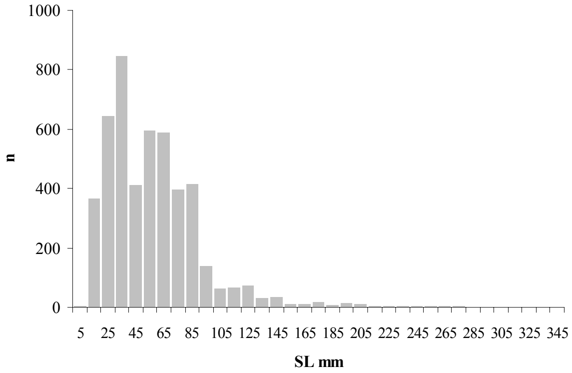
Depth profile. Night/ day net-hauls distribution



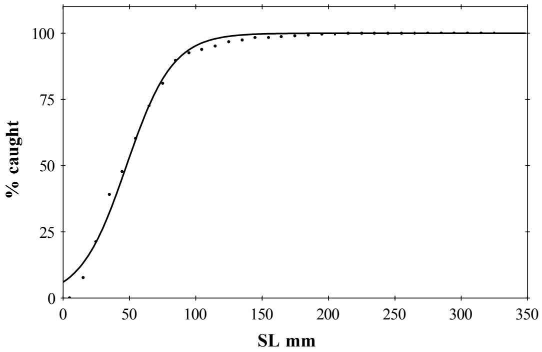
Time fishing

Standard haul basic statistics

R 2m	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	62.5	46.3	84.0	1.1	3.7	2.2	1.1	3.9
-95%	60.0	43.9	80.6	0.8	3.2	1.8	1.1	3.5
95%	64.9	48.7	87.5	1.3	4.3	2.6	1.2	4.2
min	15.0	5.0	15.0	0.0	0.2	0.0	0.2	0.9
max	322.0	322.0	322.0	74.9	121.0	76.0	7.0	20.0
std dev	35.5	35.2	50.6	3.7	8.6	5.9	0.9	5.0
std err	1.2	1.2	1.8	0.1	0.3	0.2	0.0	0.2
n	825	825	825	825	906	825	900	900



Histogram of size distribution

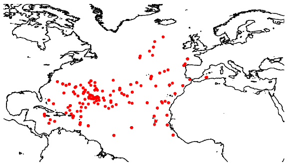


Variance explained: 99.33%;
b0 = 0.057; b1 = 47.740

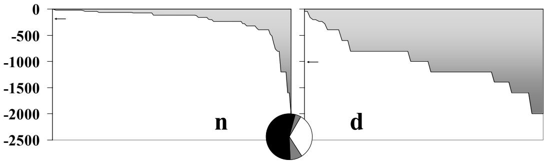
Remarks: See R3m entry. The sampler caught considerable numbers of stomiid ichthyoplankton that are preserved, unidentified in the ZMUC.

Ring net - R1.5m

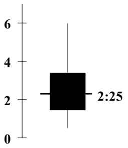
References: Schmidt, 1929; Anon, 1934; Tåning, 1944. **Institutions:** Danish Commission for Investigation of the Sea; Carlsberg Foundation; Dana Committee, Denmark. **R/Vessels:** Arkansas (ARK); Bintang (BIN); Dana (D); Dana II (DII); Ingolf (ING); Margrethe (MARG); Nordboen (NRDB); St. Jan (STJ); Texas (TEX). **Programs (regional cruises): I, II and III Dana Expeditions** (D, 20; DII, 21; DII, 21-22); **Expedition Round the World** (DII, 28-30); **Other Danish Expeditions** (ING-11-1; ARK-12-1; ING-12-1; STJ-12-1; TEX-12-1; TEX-12-2; TEX-12-3; MARG-13-1; NRDB-13-1; TEX-13-1; BIN-14-1; BIN-15-1; DII-31-1). **Data amount (n):** net hauls: **279**; records: **509**; specimens: **1123**; no_sp.: **66**. **Data quality (%):** size: **86.1**; depth: **98.6**; time fishing: **82.1**;



Geographical distribution



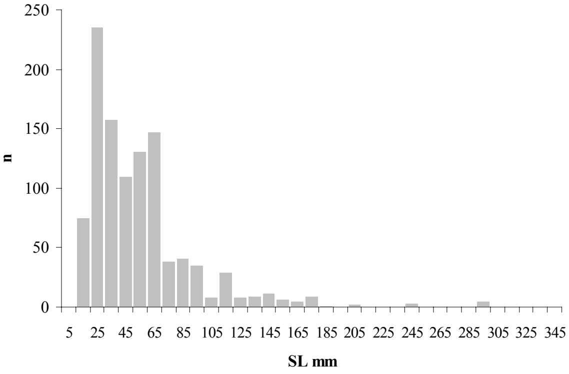
Depth profile. Night/ day net-hauls distribution



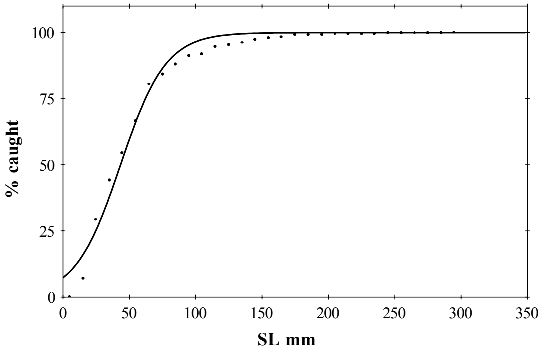
Time fishing

Standard haul basic statistics

R 1.5m	avg_sz	min_sz	max_sz	avg_wt	CPUE n	CPUE wt	sp/h	%L
mean	56.1	40.1	76.2	1.1	1.9	1.6	0.8	2.3
-95%	51.8	36.3	69.8	0.7	1.6	1.1	0.8	2.1
95%	60.3	43.8	82.7	1.5	2.2	2.2	0.9	2.6
min	11.0	11.0	11.0	0.0	0.2	0.0	0.2	0.9
max	208.3	207.0	300.0	27.1	21.5	45.8	4.0	20.0
std dev	34.3	30.6	52.4	3.2	2.7	4.7	0.6	2.1
std err	2.1	1.9	3.3	0.2	0.2	0.3	0.0	0.1
n	255	255	255	255	279	255	277	277



Histogram of size distribution



Variance explained: 98.44%;
b0 = 0.059; b1 = 43.367

Remarks: See R3m and R2m entries.

Table D.1 Distribution of net-hauls (*field_code*) by gear, biomes and provinces of Longhurst (1998b) and seasons. See Table 3.1 or List of Acronyms for full names of gears. Fig. 2.2 for full names of provinces. A: Autumn; S: Spring; SU: Summer; W: Winter; T: Total.

Gear type	*Biomes*	**POLAR**											**WESTERLY WINDS**																										
	Provinces	**BPLR**			**ARCT**				**SARC**				**NADR**					**MEDI**					**GFST**					**NAST E**					**NAST W**				
	Season	*A*	*SU*	***T***	*A*	*S*	*SU*	***T***	*A*	*S*	*SU*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***
c_mwt	**EMT 1400**																																7		36		**43**
	EMT1600	3	1	**4**	20	1		**21**		3	15	**18**	14	16	52	3	**85**									1	**1**	1	11	1	12	**25**		26			**26**
	EMT 80-630					3		**3**																79		1	**80**							4			**4**
	IYGPT																						107	11	58	93	**269**										
	YFT														18		**18**											7		12		**19**			17		**17**
m_mwt	**IKMT 10'**				2			**2**		3	5	**8**	6	5	44		**55**	17	33	21		**71**	60	4	73	15	**152**	43	16	119	5	**183**	83	88	91	57	**319**
	IKMT 10' DDS																	53		30		**83**			10	5	**15**	35		1		**36**	45	18	84	32	**179**
	MOC 10 N1																						20	20	24	17	**81**						37	17	60	26	**140**
	MOC 10																						19	19	20	13	**71**						51	26	59	41	**177**
	MOC 20 N1																						27	20	55		**102**										
	MOC 20																						57	23	73		**153**										
	R 3m						1	**1**						1	9		**10**		1	1		**2**		2	1		**3**	3	6	14		**23**	2	16	27		**45**
	RMT 8												2				**2**											13			1	**14**			8		**8**
	RMT 8 MC																											1	18	1		**21**		28	61		**89**
	RMT 10		2	**2**			4	**4**							1		**1**			2		**2**	3	1	19		**23**	25	20	29		**74**			23		**23**
	RMT 50																											30				**30**					
	TT 5																							14	18	19	**51**										
nn	**NN**														3		**3**						28	1	25		**54**	12		10		**22**	11	4	39	7	**61**
p_mwt	**IKMT 6'**																							2	1		**3**						21	5			**26**
	R 1m														1		**1**		1		1	**2**	1		3		**4**		3	2		**5**	171	139	341		**652**
	R 2m						2	**2**	1	2	1	**4**	1	21	52		**74**	11	8	25	27	**71**		8	2	1	**11**	62	24	147	2	**235**	28	53	68	2	**151**
	R 1,5m													1	17		**18**	1	1			**2**		2			**2**	5	6	21		**32**	30	34	28	1	**93**
Total		3	3	**6**	22	4	7	**33**	1	8	21	**30**	23	44	197	3	**267**	82	44	79	28	**233**	322	206	382	165	**1075**	237	104	357	20	**719**	495	458	942	166	**2062**

Table D.1 (continuation)

Gear type	*Biomes*	TRADE WIND																		COASTAL								Total
	Provinces	CARB					NATR					WTRA					ETRA				NWCS				CNRY				
	Season	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	*W*	***T***	*A*	*S*	*SU*	***T***	*A*	*S*	*SU*	***T***	*A*	*S*	*SU*	***T***	
c_mwt	**EMT 1400**																												**43**
	EMT1600							30		10	**40**		10	10	9	**29**		1		**1**							1	**1**	**251**
	EMT 80-630																					13		**13**					**100**
	IYGPT																												**269**
	YFT																												**54**
m_mwt	**IKMT 10'**	15	43	72	24	**156**	121	30	5	23	**179**	28	11	3	19	**61**		21	7	**28**	8		11	**19**	28	5		**33**	**1266**
	IKMT 10' DDS		8		14	**22**																							**335**
	MOC 10 N1			12	7	**19**																							**240**
	MOC 10			10	18	**28**																	1	**1**					**277**
	MOC 20 N1				1	**1**																	1	**1**					**104**
	MOC 20																												**153**
	R 3m	8	23	1	18	**50**	10	4	2	4	**20**	5				**5**		4		**4**			2	**2**		9		**9**	**174**
	RMT 8						3	1			**4**				1	**1**													**29**
	RMT 8 MC						2			1	**3**		1		3	**4**		1		**1**									**118**
	RMT 10	35	6	3	1	**45**	1	4			**5**		47	12		**59**													**238**
	RMT 50																												**30**
	TT 5																												**51**
nn	NN	5	1	4	1	**11**	22			6	**28**	12	1		2	**15**			3	**3**									**197**
p_mwt	**IKMT 6'**	4	17	14	14	**49**																							**78**
	R 1m			10		**10**		3		1	**4**																		**678**
	R 2m	24	91	5	90	**210**	40	50	8	14	**112**	15			2	**17**		9		**9**			2	**2**		8		**8**	**906**
	R 1,5m	19	10		25	**54**	15	28	6	10	**59**	4				**4**	1	5		**6**						9		**9**	**279**
	Total	110	199	131	213	**655**	214	150	21	69	**454**	64	70	25	36	**195**	1	41	10	**52**	8	13	17	**38**	28	31	1	**60**	**5879**

Appendix E

Checklist of the North Atlantic Stomiidae fishes

This checklist is based on information assembled in the Stomidae database (*S_db*) and in important published contributions concerning the systematics of stomiid, namely: FWNA (Bigelow et al., 1964); CLOFNAM (Hureau and Monod, 1973); and CLOFETA (Quéro et al., 1990). Additional information was obtained from several other sources as Goodyear (1980), Gibbs et al., (1983) Gomon and Gibbs (1985), Parin and Borodulina (1996, 1997b; 1998b; 2000) and Clarke (1998, 1999, 2000).

Only the type material caught at the North Atlantic is referred. The entries include: the geographical position of the station where the type(s) has been caught; the code of the collection that hold the material (Leviton et al., 1985; Leviton and Gibbs, 1988; see Appendix B) and the catalogue number; and cruise data (name of the vessel, year of capture, stations and haul-net number).

The synonyms were compiled from the sources mentioned above. The majority of the references are listed in the section Literature Cited (at the end of the thesis). However, several references, mainly published before the 20th Century, are not included in the Literature Cited, but they can be found in CLOFETA (Quéro et al., 1990). Many new references on species were added to the mentioned checklist.

Data on global distribution were compiled from ichthyological collections catalogues (i.e. USNM; ZMUC; ISH/ ZMH; BMNH; SIO; see Appendix B) and from publications referred under each species. The entries give information about species distribution outside the North Atlantic. For information on North Atlantic stomiid species distribution see the atlas in Appendix F. The global geographic data compiled were not exhaustive.

Species and authority; type material; synonyms; references; observations

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Neonesthes capensis (Gilchrist and von Bonde, 1924)

Holotype: from off South Africa; SAM 2435

Synonyms: *Astronesthes capensis* Gilchrist and von Bonde, 1924; Barnard, 1925; Smith, 1949; / *N. macrolychnus* Regan and Trewavas, 1929; Norman; 1930; Fowler, 1936; Grey, 1955; Koefoed, 1956; Nielsen, 1974; / *N. microcephalus*; Grey, 1955; / *N. nicholsi* Beebe, 1933; Beebe, 1937; Koefoed, 1956; Mead, 1958; / *N. gnathoprora* Cohen, 1956; Mead, 1958

References: Gilchrist and von Bonde, 1924; Barnard, 1925; Regan and Trewavas, 1929; Norman; 1930; Beebe, 1933; Fowler, 1936; Beebe, 1937; Smith, 1949; Grey, 1955; Cohen, 1956; Koefoed, 1956; Mead, 1958; Gibbs, 1964a; Weitzman, 1967b; Fitch and Lavenberg, 1968; Gibbs, 1968; Badcock, 1970; Geistdoerfer et al., 1971; Hulley, 1972; Kotthaus, 1972; Gibbs and Morrow, 1973; Nielsen, 1974; Badcock and Merret, 1976; Krefft, 1976; Quéro, 1978 in Maurin et al.; Parin, 1977; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984a; Fink, 1985; Gibbs, 1986c; Post, 1988; Gibbs, 1990b; Mesinger and Case, 1990; Smale et al., 1995; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: South Atlantic (from 25ºS to 40ºS). Indian (south of 25ºS; Arabian Sea) Pacific (southwestern; off Hawaii; northeastern).

Astronesthes caulophorus Regan and Trewavas, 1929

Holotype: 13º 35’ N 30º 11’ W; ZMUC P201889; “DANA” II 1921, 1162-3

Synonyms: *A. blanci* Blache and Rossignol, 1961; Blache, 1962; Blache, 1964a; Karrer, 1973; Karrer, 1975; Parin and Golovan, 1976; Parin et al., 1978; Golovan, 1978; Boltachev, 1994

References: Regan and Trewavas, 1929; Fowler, 1936; Blache and Rossignol, 1961; Blache, 1962; Karrer, 1973; Blache, 1964a; Gibbs, 1964a; Backus et al., 1965; Weitzman, 1967b; Nielsen, 1974; Parin and Golovan, 1976; Parin et al., 1978; Quéro, 1978 in Maurin et al.; Fink, 1985; Gibbs, 1986c; Gibbs, 1990b

Global distribution: South Atlantic (eastern to ca. 20ºS)

Astronesthes cyclophotus Regan and Trewavas, 1929

Syntypes (6): ZMUC P201928; P201929-30; P201931; BMNH 1929.1.4.86; 1929.1.4.87; “MARGRETHE” 1913, 1042c; 1058-4; “DANA” II 1921, 1155-3

References: Regan and Trewavas, 1929; Fowler, 1936; Gibbs, 1964a; Gibbs and Morrow, 1973; Nielsen, 1974; Gibbs, 1984a; Gibbs, 1990b; Sutton and Hopkins, 1996; Parin and Borodulina, 1998b; Parin and Borodulina, 2000

Global distribution: North Atlantic endemic.

Observations: the species was tentatively synonymised with *A. neopogon* by Parin and Borodulina (2000). In this study *A. cyclophotus* is accepted as a valid species (Chapter 5).

Astronesthes gemmifer Goode and Bean, 1896

Holotype: 44º 25’ N 53º 12’ W; USNM 24645; “POLARWAVE“ 1880, 609

References: Goode and Bean, 1896; Parr, 1927; Regan and Trewavas 1929; Roule and Angel, 1933; Beebe, 1937; Rae, 1951; Maul, 1956; Marshall, 1960; Gibbs, 1964a; Weitzman, 1967b; Backus et al., 1969; Karnella, 1969; Badcock, 1970; Rass, 1971; Gibbs and Morrow, 1973; Clarke, 1974; Parin and Golovan, 1976; Golovan, 1978; Parin et al., 1978; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984a; Gibbs and McKinney, 1988; Post, 1988; Scott and Scott, 1988; Gibbs, 1990b; Borodulina, 1994; Sutton and Hopkins, 1996; Vinnichenko, 1997; Porteiro et al., 1999; Kukuev et al., 2000; Parin and Borodulin, 2000; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (5ºS 16ºW; 11ºS 13ºE; 32ºS 45ºW). Indian (6ºS 65º E; 29º S 65ºE; central south). Pacific (23º S 180ºW, 29º S 175º W; off Hawaii).

Astronesthes leucopogon Regan and Trewavas, 1929

Syntypes (3): ZMUC P202558; P202560; BMNH 1929.1.4.107; “ST. THOMAS” 1912, 455; “DANA” II 1921, 1142-8

Synonyms: *A. longiceps* Regan and Trewavas, 1930; Gibbs, 1964a; Nielsen, 1974

References: Regan and Trewavas, 1929; Grey, 1955; Gibbs, 1964a; Weitzman, 1967b; Kotthaus, 1972; Gibbs and Morrow, 1973; Krefft, 1974; Nielsen, 1974; Kukuev, 1982; Scott and Scott, 1988; Gibbs, 1984a; Gibbs, 1990b; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (16ºS 6º W; 22ºS 2ºW; 30ºS 42ºW; 33ºS 46ºW).

Astronesthes neopogon Regan and Trewavas, 1929

Holotype: 34º 40’ N 33º 16’ W; ZMUC P201891; “DANA” II 1922, 1368-1

References: Regan and Trewavas, 1929; Fowler, 1936; Maul, 1956; Gibbs, 1964a; Weitzman, 1967b; Gibbs and Morrow, 1973; Krefft, 1974; Nielsen, 1974; Gibbs, 1984a; Gibbs, 1990b; Vinnichenko, 1997; Porteiro et al., 1999; Parin and Borodulina, 2000; Moore et al., 2003a; Wienerroither, 2003.

Global distribution: North Atlantic endemic.

Observations: *A. cyclophotus* was tentatively synonymised with this species by Parin and Borodulina (2000).

Astronesthes niger Richardson, 1844

Holotype: Habitat unknown, presumed S China Sea; BMNH 1970.5.19.1

Synonyms: *A. nigra* Richardson, 1844 / *Esox cirrhatus* Field, 1846; / *Stomias fieldii* Valenciennes in Cuvier and Valenciennes, 1849; / ? *Stomias leucopterus* Eydoux, 1850; / ? *Phaenodon ringens* Lowe, 1852; / ? *A. barbatus* Kner, 1860; Günther, 1864; Günther, 1887; / *A. myriaster* Zugmayer, 1913; Parr, 1927; Roule and Angel, 1933; Belloc, 1949; / *A. leucopogon*; Grey, 1955; / Stomiatella C Roule and Angel, 1930

References: Richardson, 1844; Valenciennes in Cuvier and Valenciennes, 1849; Lowe, 1852; Kner, 1860; Günther, 1864; Günther, 1887; Goode and Bean, 1896; Brauer, 1906; Murray and Hjort, 1912; Zugmayer, 1913; Pappenheim, 1914; Parr, 1927; Regan and Trewavas, 1929; Roule and Angel, 1930; Borodin, 1931; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Belloc, 1938; Bertin, 1940; Lozano Rey, 1947; Belloc, 1949; Poll, 1953; Albuquerque, 1954-1956; Grey, 1955; Koefoed, 1956; Marshall, 1960; Blache, 1962; Blache, 1964a; Gibbs, 1964a; Marshall, 1967; Weitzman, 1967; Badcock, 1970; Backus et al., 1970; Quéro, 1970; DeGroot and Nijssen, 1971; Rass, 1971; Kotthaus, 1972; Gibbs and Morrow, 1973; John, 1975; Krueger et al., 1977; John, 1978; Parin et al., 1978; Gibbs, 1984a; Scott and Scott, 1988; Gibbs, 1990b; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution:

Observations: Parin and Borodulina (2002) split the former *A. niger* in 8 species. Seven species of the *A. niger* species group occur in the North Atlantic and one in the Indian Ocean (see Chapter 5).

Astronesthes richardsoni (Poey, 1853)

Holotype: 23º 40' N 79º 18' W; NMW 59088; Position estimated (off Cuba); apparently lost; no cruise data

Synonyms: *Chauliodus richardsoni*; / *A. filifer* Regan and Trewavas, 1929; Norman, 1930; Fowler, 1936; Bertin, 1940; Blache, 1962; Blache, 1964a; Nielsen, 1974; Lloris, 1986; / *A. oculatus* Regan and Trewavas, 1929; Nielsen, 1974

References: Poey, 1853; Poey, 1875; Günther, 1864; Parr, 1927 (part); Regan and Trewavas, 1929; Norman, 1930; Fowler, 1936; Bertin, 1940; Blache, 1962; Blache, 1964a; Gibbs, 1964a; Backus et al., 1965; Weitzman, 1967b; Karnella, 1969; Backus et al., 1970; Rass, 1971; Krefft, 1974; Parin et al., 1974; Nielsen, 1974; Bekker et al., 1975, Parin and Golovan, 1976; Parin et al., 1978; Murdy et al., 1983; Lloris, 1986; Gibbs, 1990b; Borodulina, 1994; Boltachev, 1994; Sutton and Hopkins, 1996; Parin and Borodulina, 2000; Moore et al., 2003a

Global distribution: South Atlantic (eastern to ca. 20ºS; 27ºS 38ºW; 25ºS 37ºW; 33ºS 39ºW).

Astronesthes similis Parr, 1927

Holotype: 24º 29' N 77º 29' W; YPM 2098; "PAWNEE" 1927, 23

Synonyms: *A. similus*; Moore et al., 2003a

References: Parr, 1927; Regan and Trewavas, 1930; Bertin, 1940; Marshall, 1960; Gibbs, 1964a; Weitzman, 1967b; Karnella, 1969; Backus et al., 1970; Rass, 1971; Bekker et al., 1975; Belyanina, 1975; Murdy et al., 1983; Gibbs and Amaoka, 1984; Fink, 1985; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (10ºS 27ºW; 16ºS 30ºW; 23ºS 33ºW; 25ºS 36ºW).

Astronesthes zharodi Parin and Borodulina, 2000

Holotype: 00º 20' N 25º 20' W; ISH 803-1968; "WALTHER HERWIG" 1968, 15-I/ 68

References: Parin and Borodulina, 2000

Global distribution: Eastern Tropical Atlantic.

Astronesthes atlanticus Parin and Borodulina, 1996

Holotype: 25º 09' N 58º 07' W; USNM 333306; “ANTON DOHRN”, 1979, 170-I/ 79

Synonyms: *A. indicus* (non Brauer, 1906); Parr, 1927; Regan and Trewavas, 1929; Norman, 1930; Fowler, 1936; Bertin, 1940; Blache, 1962; Gibbs, 1964a; Karnella, 1969; Badcock, 1970; Krefft, 1974; Parin et al., 1974; Bekker et al., 1975; Murdy et al., 1983; Gibbs, 1984a; Gibbs, 1990b; Sutton and Hopkins, 1996

References: Parr, 1927; Regan and Trewavas, 1929; Norman, 1930; Fowler, 1936; Bertin, 1940; Blache, 1962; Gibbs, 1964a; Karnella, 1969; Badcock, 1970; Krefft, 1974; Parin et al., 1974; Bekker et al., 1975; Murdy et al., 1983; Gibbs, 1984a; Gibbs, 1990b; Parin and Borodulina, 1996; Sutton and Hopkins, 1996; Wienerroither, 2003

Global distribution: South Atlantic (to 34ºS, mostly in central and eastern).

Astronesthes macropogon Goodyear and Gibbs, 1970

Holotype: 23º 50' N 20º 08' W; ISH 201-1966; “WALTHER HERWIG” 1966, 180b/ 66

Synonyms: *A. cyaneus* (non Brauer, 1906); Parr, 1927; Regan and Trewavas, 1930 (part); Norman, 1930; Fowler, 1936; Blache, 1962; Blache, 1964a; Gibbs, 1964a (part); Backus et al., 1965

References: Parr, 1927; Regan and Trewavas, 1930 (part); Norman, 1930; Fowler, 1936; Blache, 1962; Blache, 1964a; Gibbs, 1964a (part); Backus et al., 1965; Goodyear and Gibbs, 1970; Nielsen, 1974; Parin et al., 1974; Bekker et al., 1975; Parin and Golovan, 1976; Krefft, 1978; Parin et al., 1978; Kukuev, 1982; Uyeno et al., 1983; Gibbs, 1984a; Gibbs, 1990b; Sutton and Hopkins, 1996; Parin and Borodulina, 1997; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (eastern to 7ºS; between 23ºS 33ºW and 35ºS 47ºW).

Astronesthes micropogon Goodyear and Gibbs, 1970

Holotype: 01º 58' N 04º 00' W; USNM 203612; “REINE POKOU” 1962, 471

Synonyms: *A. cyaneus* (non Brauer, 1906); Regan and Trewavas, 1930 (part); Fowler, 1936 (part); Gibbs, 1964a (part); Weitzman, 1967b

References: Regan and Trewavas, 1930; Fowler, 1936; Gibbs, 1964a; Weitzman, 1967b; Goodyear and Gibbs, 1970; Nielsen, 1974; Parin et al., 1974; Bekker et al., 1975; Krefft, 1978; Murdy et al., 1983; Gibbs, 1984a; Gibbs, 1990b; Sutton and Hopkins, 1996; Parin and Borodulina, 1997; Porteiro et al., 1999; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (to 7ºS; between 25ºS and 26ºS 27ºW)

Borostomias antarcticus (Lönnberg, 1905)

Holotype: Type from southern hemisphere (48º 27' S 42º 36' W); NRMS 11001

Synonyms: *Astronesthes antarticus* Lönnberg, 1905 / *B. macrophthalmus* Regan and Trewavas, 1929; Krefft, 1963; / *B. roulei* Regan and Trewavas, 1929 / *Diplolychnus bifilis* Regan and Trewavas, 1929; Koefoed, 1956; Krefft, 1963; / *B. macrophthalmoides* Koefoed, 1956 / *Astronesthes richardsoni* (misident.); Goode and Bean, 1896; Brauer, 1906; Holt and Byrne, 1906; Holt and Byrne, 1910; Holt and Byrne, 1913; Gilchrist and von Bonde, 1924; Smith, 1949 / *B. richardsoni*; Barnard, 1925; Roule and Angel, 1933; *A. elucens*; Parr, 1927 (misident.)

References: Goode and Bean, 1896; Lönnberg, 1905; Brauer, 1906; Holt and Byrne, 1906; Holt and Byrne, 1910; Holt and Byrne, 1913; Gilchrist and von Bonde, 1924; Barnard, 1925; Parr, 1927; Regan and Trewavas, 1929; Norman, 1930; Roule and Angel, 1933; Smith, 1949; Koefoed, 1956; Gibbs, 1964a; Krefft, 1964; Bussing, 1965; Weitzman, 1967b; Gibbs, 1968; Geistdoerfer et al., 1971; Tortonese and Sertorio, 1974; Krueger et al., 1977; Gushchin and Kukuev, 1981; Matallanas, 1982; Gibbs, 1984a; Fink, 1985; McKelvie and Haedrich, 1985; Gibbs, 1986c; Swinney et al., 1986; Post, 1988; Magnússon, 1996; Vinnichenko, 1997; Figueroa et al., 1998; Kukuev et al., 2000; Alpoim et al., 2002; Kukuev and Trunov, 2002; Sigurðsson et al., 2002; Moore et al., 2003a; Moore et al., 2003b; Fock et al., 2004

Global distribution: Southern Subtropical Convergence (Circum-global south of 30ºS)

Borostomias elucens (Brauer, 1906)

Holotype: 00º 55' N 04º 37' W; ZMB: 17431; “VALDIVIA” 1898, 51

Synonyms: *B. braueri* Regan, 1908; Regan and Trewavas, 1929; Briggs, 1958 / *B. macristius* Regan and Trewavas, 1929; Cadenat, 1961; Blache, 1964a / *B. schmidti* Regan and Trewavas, 1929; Myers, 1934; / *Elapterostomias philippinus* Fowler, 1934; / *Astronesthes elucens* Brauer, 1906; Parr, 1927 (part); Fowler, 1934

References: Brauer, 1906; Regan, 1908; Regan and Trewavas, 1929; Parr, 1927; Fowler, 1934; Myers, 1934; Springer and Bullis, 1956; Briggs, 1958; Cadenat, 1961; Blache, 1962; Blache, 1964a; Gibbs, 1964a; Weitzman, 1967b; Rass, 1971; Parin et al., 1974; Bekker et al., 1975; Parin 1975; Parin, 1976; Parin and Golovan, 1976; Parin et al, 1977; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Uyeno et al., 1983; Gibbs, 1984a; Fink, 1985; Gibbs, 1990b; Sutton and Hopkins, 1996

Global distribution: South Atlantic (to 16ºS). Indian (from 3ºN to 13ºS; eastern tropical). Indo-Pacific. Pacific (from Japan to Tasman Sea; Eastern Tropical Pacific).

Observations: According to Eschmeyer (1998) Brauer's holotype of *B. elucens* is ZMB (=ZMHU) 17431 but apparently it was lost.

Borostomias mononema (Regan and Trewavas, 1929)

Syntypes (2): ZMUC P202858; BMNH 1929.1.4.121; "DANA" II 1922, 1279-1; "DANA" II 1922, 1281-1

Synonyms: *Diplolychnus mononema* Regan and Trewavas, 1929; Fraser-Brunner, 1931; Fowler, 1936; Norman, 1939; Blache, 1962; Gibbs, 1964a; Roux and Hureau, 1969; Badcock, 1970; Rass, 1971; Nielsen, 1974; Parin et al., 1974; / *D. lucifer* Regan and Trewavas, 1929; Fowler, 1936; Gibbs, 1964a; Nielsen, 1974

References: Regan and Trewavas, 1929; Fraser-Brunner, 1931; Fowler, 1936; Norman, 1939; Blache, 1962; Gibbs, 1964a; Weitzman, 1967b; Roux and Hureau, 1969; Badcock, 1970; Rass, 1971; Gibbs and Morrow, 1973; Karrer, 1973; Nielsen, 1974; Parin et al., 1974; Parin and Golovan, 1976; Parin et al., 1977; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Uyeno et al., 1983; Gibbs, 1984a; Gibbs, 1990b; Smale et al., 1995; Sutton and Hopkins, 1996; Wienerroither, 2003

Global distribution: South Atlantic (eastern to 5ºS and 28ºS). Indian (western equatorial). Indo-Pacific Pacific (from south China to Australia and New Zealand).

Heterophotus ophistoma Regan and Trewavas, 1929

Syntypes (6): ZMUC P202081; P202859; P202860; P202861; P202862; BMNH 1929.1.4.122; "DANA" II 1921, 1163-3, 1166-2, 1168-3; "DANA" II 1922, 1202-1, 1217-4 , 1285-2

References: Regan and Trewavas, 1929; Fowler, 1936; King and Iversen, 1962; Gibbs, 1964a; Backus et al., 1965; Weitzman, 1967a; Karnella, 1969; Rass, 1971; Clarke, 1974; Krefft, 1974; Bekker et al., 1975; Parin, 1975; Parin et al., 1976; Parin et al., 1977; Parin, 1978; Uyeno et al., 1983; Fink, 1985; Gibbs, 1990b; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic. Indian. Pacific (southeastern, southwestern, northwestern and central north).

Rhadinesthes decimus (Zugmayer, 1911)

Holotype: 44º 24' N 11º 36' W; MOM: 91 0959; "PRINCESSE ALICE" II 1910, 3001

Synonyms: *Astronesthes decimus* Zugmayer, 1911; Belloc, 1949; / *R. jacobssoni* Nybelin, 1947; Koefoed, 1956; / *R. lucberti* Blanc and Blache, 1963; Geistdoerfer et al., 1971

References: Zugmayer, 1911; Regan and Trewavas, 1929; Lozano Rey, 1947; Nybelin, 1947; Belloc, 1949; Koefoed, 1956; Blanc and Blache, 1963; Gibbs, 1964a; Weitzman, 1967; Quéro, 1969; Geistdoerfer et al., 1971; Gibbs and Morrow, 1973; Krefft, 1976; Parin and Golovan, 1976; Golovan, 1978; Gushchin and Kukuev, 1981; Gibbs, 1984a; Fink, 1985; Gibbs, 1990b; Magnússon, 1996; Sigurðsson et al., 2002; Wienerroither, 2003

Global distribution: South Atlantic (to 3ºS; 16ºS 6ºW; 30º -34ºS, 40º - 47ºW). Indian (2ºN - 12ºS 59º - 65ºE). Indo-Pacific. Pacific (7ºN - 16ºS 135º - 153ºE; 3ºN - 12ºS 125º - 143ºW; off Hawaii).

Chauliodus sloani Bloch and Schneider, 1801

Holotype: 36º N 5º 25' W; Gibraltar, position estimated; BMNH 1978.9.11.1; no cruise data

Synonyms: *C. setinosus* Bloch and Schneider, 1801; Bonaparte, 1832-1841; Bonaparte, 1845; / *Esox stomias* Shaw, 1804 / *Stomias boa* (*C. schneideri*); Cuvier, 1817 / *Stomias schneideri;* Risso, 1826; Cuvier, 1836-1849 / *Leptodes sloanii*; Swainson, 1839; / *C. dentatus* Garman, 1899; Beebe, 1929 / *C. dannevigi* McCulloch, 1916; Regan and Trewavas, 1929 / *C. atlantis* Barbour, 1942 (part) / *C. sloanei dannevigi* Ege, 1948; Haffner, 1952; / *C. sloanei sloanei* Ege, 1948; Haffner, 1952; Koefoed, 1956; / *C. sloanei secundus* Ege, 1948; Haffner, 1952; / *C. danae* (misident.); Phillipps, 1942

References: Bloch and Schneider, 1801; Shaw, 1804; Cuvier, 1817; Risso, 1826; Cuvier, 1836-1849; Bonaparte, 1832-1841; Swainson, 1839; Bonaparte, 1845; Valenciennes in Cuvier and Valenciennes, 1849; Günther, 1864; Leuckart, 1865; Canestrini, 1872; Doderlein, 1878-1879; Goode and Bean, 1879; Leydig, 1879; Goode, 1880; Jordan and Gilbert, 1882; Facciolà, 1883; Jordan, 1885; Vincinguerria, 1885; Günther, 1887; Agassiz, 1888; Vaillant, 1888; Alcock, 1889; Collett, 1890; Alcock, 1899; Carus, 1893; Goode and Bean, 1896; Jordan and Evermann, 1896; Alcock, 1899; Garman, 1899; Jordan and Starcks, 1904; Lo Bianco, 1902; Odón de Buen, 1902; Richard, 1905; Brauer, 1906; Brauer, 1908; Regan, 1908; Zugmayer, 1911; Murray and Hjort, 1912; Weber, 1913; Weber and Beaufort, 1913; Bierbaum, 1914; Pappenheim, 1914; Sanzo, 1914; Gilbert, 1915; McCulloch, 1916; Sanzo, 1918; Roule, 1919; Gilchrist, 1921; Gilchrist, 1922; Saemundsson, 1922; Regan, 1923; Roule and Angel, 1924; Barnard, 1925; Skowron, 1928; Beebe, 1929; Regan and Trewavas, 1929; Jordan, Evermann and Clark, 1930; Norman, 1930 (part); Roule and Angel, 1930; Borodin, 1931; Gregory, 1933; Zugmayer, 1933; Fowler, 1936; Beebe, 1937; Parr, 1937; Bertin, 1940; Norman, 1939; Barbour, 1942; Ferreira, 1942; Phillipps, 1942; Ege, 1948; Maul, 1948; Nybelin, 1948; Soljan, 1948; Tchernavin, 1948; Haffner, 1952; Bigelow and Schroeder, 1953; Tchernavin, 1953; Collins, 1954; Albuquerque, 1954-1956; Marshall, 1954; Grey, 1955; Munro, 1955; Koefoed, 1956; Denton and Marshall, 1958; Andriashev, 1961; Morrow, 1961; Smith, 1961; Ochiai and Asano, 1963; Blache, 1964b; Morrow, 1964a; Backus et al., 1965; Bussing, 1965; Crane, 1966; Gibbs and Hurwitz, 1967; Kotthaus, 1967; Weitzman, 1967b; Gibbs, 1968; Monod, 1968; Trunov, 1968; Backus et al., 1969; Halliday and Scott, 1969; Karnella, 1969; Quéro, 1969; Badcock, 1970; Craddock and Mead, 1970; Bradbury et al., 1971; Geistdoerfer et al., 1971; Marshall, 1971; Ueno, 1971; Kotthaus, 1972; Musick, 1973; Parin et al., 1973; Morrow, 1973a; Parin and Novikova, 1974; Parin et al., 1974; Bekker et al., 1975; Badcock and Merret, 1976; Dias et al., 1976; Jahn and Backus, 1976; Parin and Golovan, 1976; Belyanina, 1977; Quéro, 1978 in Maurin et al.; Lloris and Rucabado, 1979; Gushchin and Kukuev, 1981; Kukuev, 1982; Murdy et al., 1983; Uyeno et al., 1983; Gibbs, 1984b; Kawaguchi and Moser, 1984; Roe and Badcock, 1984; Fink, 1985; McKelvie and Haedrich, 1985; Gibbs, 1986b; Lloris, 1986; Swinney et al., 1986; Scott and Scott, 1988; Papaconstantinou, 1990; Parin, 1990; Brooks and Saenger, 1991; Okamura et al., 1995; Smale et al., 1995; Magnússon, 1996; Sutton and Hopkins, 1996; Vinnichenko, 1997; Wagner et al., 1998; Kukuev et al., 2000; Alpoim et al., 2002; Kukuev, 2002; Kukuev and Trunov, 2002; Sigurðsson et al., 2002; Moore et al., 2003a; Wienerroither, 2003; Fock et al., 2004

Global distribution: South Atlantic. Southern Subtropical Convergence. Indian (south of 10ºN). Indo-Pacific. Pacific (western from 40ºS to 40ºN; equatorial central; north of Hawaii; southeastern to 30ºS).

Chauliodus schmidti Ege, 1948

Holotype: 13º 31' N 18º 03' W; ZMUC P203240; "DANA" II 1930, 4005-7

Synonyms: *C. sloanei* (non Schneider, 1801); Norman, 1930 (part) / *C. sloani* (non Schneider, 1801); Poll, 1953

References: Norman, 1930; Ege, 1948; Poll, 1953; Morrow, 1961; Blache, 1964b; Backus et al., 1965; Crane, 1966; Karnella, 1969; Backus et al., 1970; Krefft, 1974; Parin and Novikova, 1974; Parin et al., 1974; Parin and Golovan, 1976; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Parin, 1990

Global distribution: South Atlantic (eastern to 15º S and 30ºW)

Chauliodus danae Regan and Trewavas, 1929

Syntypes (1015): from 150 stations; ZMUC (see Nielsen, 1974)

Synonyms: ? *C. barbatus* (non Garman); Belloc, 1938; / *C. atlanticus*; Barbour, 1942 (part)

References: Regan and Trewavas, 1929; Norman, 1930; Borodin, 1931; Fowler, 1936; Beebe, 1937; Parr, 1937; Belloc, 1938; Bertin, 1940; Barbour, 1942; Ege, 1948 (part); Nybelin, 1948; Haffner, 1952; Dollfus, 1955; Grey, 1955; Albuquerque, 1954-1956; Koefoed, 1956; Morrow, 1961; Morrow, 1964a; Crane, 1966; Backus et al., 1965; Backus et al., 1969; Backus et al., 1970; Badcock, 1970; Geistdoerfer et al., 1971; Kotthaus, 1972; Morrow, 1973a; Krefft, 1974 (part); Parin and Novikova, 1974; Bekker et al., 1975; Badcock and Merret, 1976; Quéro, 1978 in Maurin et al.; Kukuev, 1982; Gibbs, 1984b; Kawaguchi and Moser, 1984; Roe and Badcock, 1984; Fink, 1985; Scott and Scott, 1988; Parin, 1990; Brooks and Saenger, 1991; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: North Atlantic endemic.

Stomias brevibarbatus Ege, 1918

Syntypes (5): ZMUC P202164; P203235; P203236; P203237; P203238; "MARGRETHE" 1913, 1043-5; 1043-6; 1058-4; 1063-4; 1067-5

References: Ege, 1918; Parr, 1931; Ege, 1934; Fowler, 1936; Beebe, 1937; Maul, 1948; Grey, 1955; Maul, 1956; Nicol, 1960; Morrow, 1964b; Gibbs, 1969; Badcock, 1970; Morrow, 1973b; Nielsen, 1974; Shcherbachev and Novikova, 1976; Kukuev, 1982; Gibbs, 1984c; Fink, 1985; Fink and Fink, 1986; Scott and Scott, 1988; Gibbs, 1990a; Haygood et al., 1994; Sutton and Hopkins, 1996; Vinnichenko, 1997; Porteiro et al., 1999; Kukuev, 2002; Moore et al., 2003a; Wienerroither, 2003

Global distribution: North Atlantic endemic.

Stomias longibarbatus Brauer, 1902

Holotype: southeastern Gulf of Guinea; ZMHU 17446; "VALDIVIA" 1902, 57

Synonyms: *Macrostomias longibarbatus* Brauer, 1902; Brauer, 1906; Murray and Hjort, 1912; Norman, 1930; Borodin, 1931; Beebe, 1933; Fowler, 1936; Grey, 1955; Koefoed, 1956; Mead, 1958; Blache, 1962; Morrow, 1964b; Kotthaus, 1967; Gibbs, 1968; Karnella, 1969; Badcock, 1970; Blache et al., 1970; Craddock and Mead, 1970; Morrow, 1973b; Clarke, 1974; Parin, 1975; Parin et al., 1976; Shcherbachev and Novikova, 1976; Parin et al., 1977; Parin et al., 1978; Kukuev, 1982; Gibbs, 1984c; Kawaguchi and Moser, 1984; Gibbs, 1986a; Figueroa et al., 1998; / *Macrostomias calosoma* Beebe, 1933; Mead, 1958 / *M. furcatus* Shcherbachev and Novikova, 1976; / *Macrostomias longibarba*; Gibbs, 1968; / *Macrostomias congibarbatus* (misspelling); Vinnichenko, 1997

References: Brauer, 1902; Brauer, 1906; Murray and Hjort, 1912; Ege, 1918; Norman, 1930; Borodin, 1931; Beebe, 1933; Fowler, 1936; Grey, 1955; Koefoed, 1956; Mead, 1958; Blache, 1962; Morrow, 1964b; Kotthaus, 1967; Gibbs, 1969; Karnella, 1969; Badcock, 1970; Blache et al., 1970; Craddock and Mead, 1970; Morrow, 1973b; Clarke, 1974; Parin, 1975; Fink and Fink, 1986; Parin et al., 1976; Shcherbachev and Novikova, 1976; Parin et al., 1977; Parin et al., 1978; Kukuev, 1982; Gibbs, 1984c; Gibbs, 1986a; Fink, 1985; Fink and Fink, 1986; Gibbs, 1990a; Sutton and Hopkins, 1996; Vinnichenko, 1997; Figueroa et al., 1998; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (to 6ºS; and from 20º to 43ºS). Indian (equatorial). Indo-Pacific. Pacific (from off Japan to Australia and New Zealand; equatorial; southeastern off Chile)

Stomias lampropeltis Gibbs, 1969

Syntypes: 55 specimens from the southeastern Atlantic; MNHN

Synonyms: *S. colubrinus* (non Garman, 1899); Brauer, 1906; Ege, 1918; Beebe, 1929; Norman, 1930; Ege, 1934 (part); Bruun, 1936; Fowler, 1936; Bruun, 1958; Marshall, 1960; Cadenat, 1961; Blache, 1962; Morrow, 1964b; (part) / non *S. hexagonatus*; Borodin, 1931 / *S. colubrinus orientalis* Blache, 1964c; Blache et al., 1970

References: Brauer, 1906; Ege, 1918; Beebe, 1929; Norman, 1930; Borodin, 1931; Ege, 1934 (part); Bruun, 1936; Fowler, 1936; Bruun, 1958; Marshall, 1960; Cadenat, 1961; Blache, 1962; Blache, 1964c; Morrow, 1964b (part); Gibbs, 1969; Blache et al., 1970; Karrer, 1973; Krefft, 1974; Parin and Golovan, 1976; Shcherbachev and Novikova, 1976; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Fink, 1985; Fink and Fink, 1986; Gibbs, 1990a

Global distribution: South Atlantic (eastern to 16ºS)

Observations: the species *S. lampropeltis* Gibbs, 1969 is a substitute name for the *S. colubrinus orientalis* Blache, 1964c; therefore the syntypes are those used by the late author to describe his sub-species.

Stomias boa boa (Risso, 1810)

Stomias boa ferox Reinhardt, 1843

Holotype: no data

Synonyms (*S. boa boa*): Esox boa Risso, 1810; / S. boa; Cuvier, 1817; Cuvier, 1829; Wienerroither, 2003; / S. barbatus Bonaparte, 1832-1841; / Stomiasunculus barbatus; Kaup, 1860; Günther, 1870; / S. hexagonatus (part) Garman, 1899; / S. bonapartei Fowler, 1911; / S. elongatus atlanticus Pappenheim, 1914; / S. atlanticus Norman, 1930

Synonyms (*S. boa ferox*): *S. ferox* Reinhardt, 1843; Kroyer, 1847; Gaimard, 1842-1856; Gill, 1862; Günther, 1864; Jordan and Gilbert, 1882; Goode and Bean, 1883; Günther, 1887; Jordan, 1887; Lütken, 1892; Goode and Bean, 1896; Jordan and Evermann, 1896; Ege, 1918; Jordan, Evermann and Clark, 1930; Norman, 1930; Beebe, 1937; Bigelow and Schroeder, 1953; / *S. fusus* Beebe, 1929; Parr, 1931; Mead, 1958; / *S. elongatus;* Borodin, 1931; / *Stomioides nicholsi* Parr, 1933; / S. boa; Vaillant, 1888; Koehler, 1896; Collett, 1905; Brauer, 1906; Holt and Byrne, 1906; Holt and Byrne, 1907; Hjort, 1911; Zugmayer, 1911; Holt and Byrne, 1913; Murray and Hjort, 1912; Vaillant, 1919; Beebe, 1929; Borodin, 1931; Parr, 1931; Roule and Angel, 1933; / *S. boa boa*; Alpoim et al., 2002

References: Risso, 1810; Cuvier, 1817; Cuvier, 1829; Bonaparte, 1832-1841; Gaimard, 1842-1856; Reinhardt, 1843; Kroyer, 1847; Kaup, 1860; Gill, 1862; Günther, 1864; Günther, 1870; Jordan and Gilbert, 1882; Goode and Bean, 1883; Günther, 1887; Jordan, 1887; Vaillant, 1888; Lütken, 1892; Goode and Bean, 1896; Jordan and Evermann, 1896; Koehler, 1896; Garman, 1899; Collett, 1905; Brauer, 1906; Holt and Byrne, 1906; Holt and Byrne, 1907; Fowler, 1911; Hjort, 1911; Zugmayer, 1911; Holt and Byrne, 1913; Murray and Hjort, 1912; Sanzo, 1912; Pappenheim, 1914; Ege, 1918; Sanzo, 1918; Beebe, 1929; Jordan, Evermann and Clark, 1930; Norman, 1930; Borodin, 1931; Parr, 1931; Parr, 1933; Roule and Angel, 1933; Ege, 1934; Brunn, 1936; Beebe, 1937; Nybelin, 1948; Bigelow and Schroeder, 1953; Karlovac, 1953; Grey, 1955; Koefoed, 1956; Maul, 1956; Demir, 1958; Rimbault, 1963; Tortonese, 1963; Blache, 1964c; Morrow, 1964b; Weitzman, 1967b; Gibbs, 1968; Backus et al., 1969; Gibbs, 1969; Halliday and Scott, 1969; Backus et al., 1970; Badcock, 1970; Geistdoerfer et al., 1971; Musick, 1973; Jahn and Backus, 1976; Parin and Golovan, 1976; Shcherbachev and Novikova, 1976; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984c; Kawaguchi and Moser, 1984; Roe and Badcock, 1984; Fink, 1985; McKelvie and Haedrich, 1985; Fink and Fink, 1986; Gibbs, 1986a; Swinney et al., 1986; Scott and Scott, 1988; Gibbs, 1990a; Papaconstantinou, 1990; Okamura et al., 1995; Smale et al., 1995; Magnússon, 1996; Vinnichenko, 1997; Figueroa et al., 1998; Kukuev et al., 2000; Alpoim et al., 2002; Kukuev, 2002; Sigurðsson et al., 2002; Moore et al., 2003a; Moore et al., 2003b; Wienerroither, 2003; Fock et al., 2004

Global distribution (*S. b. boa*): South Atlantic (to 15ºS) Circumglobal between 30ºS and 45º S.

Global distribution (*S. b. ferox*): North Atlantic endemic.

Observations: *S. boa* is the unique stomiid species that has two recognised sub-species. The sub-species were described as different species but Ege (1934) synonymised the two forms.

Stomias affinis Günther, 1887

Holotype: 18º N 60º 20' W (S of Sombrero Island, position estimated; BMNH 1887.12.7.24; "CHALLENGER" 1873, 23

Synonyms: *S. elongatus* Wood-Mason and Alcock, 1891; Goode and Bean, 1896; Alcock, 1899; Brauer, 1906; Norman, 1930; Parr, 1931 / *S. valdiviae* Brauer, 1906; Weber and Beaufort, 1913; Ege, 1918; Beebe, 1929; Parr, 1931; Parr, 1937 / *Pseudeustomias myersi* Fowler, 1934

References: Günther, 1887; Wood-Mason and Alcock, 1891; Goode and Bean, 1896; Jordan and Evermann, 1896; Alcock, 1899; Brauer, 1906; Weber and Beaufort, 1913; Pappenheim, 1914; Ege, 1918; Beebe, 1929; Jordan, Evermann and Clark, 1930; Norman, 1930; Parr, 1931; Ege, 1934; Fowler, 1934; Bruun, 1936; Fowler, 1936; Parr, 1937; Belloc, 1938; Norman, 1939; Kuroda, 1951; Poll, 1953; Springer and Bullis, 1956; Imai, 1957; Marshall, 1960; Cadenat, 1961; Blache, 1962; Marshall, 1963; Blache, 1964c; Marshall and Bourne, 1964; Morrow, 1964b; Backus et al., 1965; Weitzman, 1967b; Aron and Goodyear, 1969; Gibbs, 1969; Karnella, 1969; Backus et al., 1970; Blache et al., 1970; Bradbury et al., 1971; Rass, 1971; Parin et al., 1973; Parin et al., 1974; Bekker et al., 1975; Parin, 1975; Shcherbachev and Novikova, 1976; Parin and Golovan, 1976; Parin, 1976; Parin et al., 1977; Parin et al., 1978; Zama and Yasuda, 1979; Uyeno et al., 1983; Fink, 1985; Fink and Fink, 1986; Gibbs, 1990a; Sutton and Hopkins, 1996; Moore et al., 2003a; Moore et al., 2003b

Global distribution: South Atlantic (to 20ºS). Indian (between 10º N and 5º S). Indo-Pacific. Pacific (from Japan to Australia; equatorial central).

Chirostomias pliopterus Regan and Trewavas, 1930

Syntypes (3): ZMUC P201941; P201942; P201943; “THOR” 1906, 38-06; “DANA” 1921, 928; “DANA” II 1922, 1377-4

Synonyms: *C. lucidimanus* Beebe, 1932c; Mead, 1958

References: Regan and Trewavas, 1930; Beebe, 1932c; Beebe, 1933a; Fowler, 1936; Schroeder, 1940; Lozano Rey, 1949; Beebe, 1937; Beebe and Crane, 1939; Lozano Rey, 1947; Grey, 1955; Morrow and Gibbs, 1964; Weitzman, 1967b; Morrow, 1973c; Nielsen, 1974; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984b; Fink, 1985; Scott and Scott, 1988; Gibbs and Barnett, 1990; Vinnichenko, 1997; Sigurðsson et al., 2002; Moore et al., 2003a; Wienerroither, 2003

Global distribution: North Atlantic endemic.

Trigonolampa miriceps Regan and Trewavas, 1930

Holotype: 48º 42' N 12º 20' W; ZMUC P208240; “THOR” 1906, 52

References: Regan and Trewavas, 1930; Parr, 1933; Beebe and Crane, 1939; Bigelow and Schroeder, 1953; Koefoed, 1956; Wellerhaus, 1963; Morrow and Gibbs, 1964; Weitzman, 1967b; Gibbs, 1968; Craddock and Mead, 1970; Parin, 1971; Morrow, 1973c; Parin et al., 1973; Krefft, 1974; Gueguen et al., 1975; Krefft, 1976; Quéro, 1978 in Maurin et al.; Quéro, 1979 in Tortonese and Hureau; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984d; Fink, 1985; Gibbs, 1986d; Post, 1988; Gibbs and Barnett, 1990; Smale et al., 1995; Magnússon, 1996; Vinnichenko, 1997; Figueroa et al., 1998; Porteiro et al., 1999; Kukuev et al., 2000; Hartel and Craddock, 2002; Sigurðsson et al., 2002; Moore et al., 2003a

Global distribution: Southern Subtropical Convergence (Atlantic: between 33ºS and 41ºS; Indian and Pacific: 35ºS and 47ºS).

Thysanactis dentex Regan and Trewavas, 1930

Syntypes (5): ZMUC P202078; P202079; P202080; BMNH 1929.7.6.8; 1929.7.6.9; “DANA” II 1921, 1165-8, 1180-2, 1183-5, 1185-3, 1184-4

References: Regan and Trewavas, 1930; Fowler, 1936; Beebe and Crane, 1939; King and Iversen, 1962; Morrow and Gibbs, 1964; Grandperrin and Rivaton, 1966, Gibbs, 1968; Karnella, 1969; Blache et al., 1970; Fourmanoir, 1970; Rass, 1971; Parin et al., 1973; Clarke, 1974; Nielsen, 1974; Parin et al., 1974; Parin, 1975; Parin and Sokolovsky, 1976; Parin et al., 1976; Parin et al., 1977; Jorensen and Munk, 1979; Fink, 1985; Gibbs and Barnett, 1990

Global distribution: South Atlantic (to 7ºS, 33ºW - 5ºE; 18ºS 4ºW; 30ºS 5ºE) Pacific (southeastern tropical; off northeastern Australia; northeastern to 26ºN 146ºW; central equatorial; off Hawaii).

Leptostomias bilobatus (Koefoed, 1956)

Neotype (1): 29º 08' N 25º 16' W; FMNH 65610; “OREGON” 1959, 2573;

Synonyms: *Melanostomias bilobatus* Koefoed, 1956

References: Koefoed, 1956; Morrow and Gibbs, 1964; Karnella, 1969; Rass, 1971; Krueger et al., 1977; Quéro, 1978 in Maurin et al.; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (35ºS 40ºW). Indian (10º - 12ºS 65ºE; tentatively).

Observations: the neotype was described by Morrow and Gibbs (1964); according the authors the holotype ("Michael Sars", North Atlantic Exedition 1910), was lost during a fire. The Indian Ocean species needs further verification.

Leptostomias gladiator (Zugmayer, 1911)

Holotype: 44º 19' N 11º 19' W; MOM: 91 1130; "PRINCESSE ALICE" II 1910, 3003

Synonyms: *Nematostomias gladiator* Zugmayer, 1911; Belloc, 1949; / *Melanostomias gladiator*; Parr, 1927; Roule and Angel, 1933 / *L. cf. gladiator*; Parin and Sokolovsky, 1976; / *Melanostomias problematicus* Parr, 1927 / *L. problematicus*; Regan and Trewavas, 1930; / *L. ramosus* Regan and Trewavas, 1930; Beebe, 1933a; Springer and Bullis, 1956; Nielsen, 1974; / *M. ramosus*; Fowler, 1936; Lozano Rey, 1947; *Leptostomias* sp. 2; Parin et al., 1977; / *Leptostomias* sp. 4; Parin et al., 1977

References: Zugmayer, 1911; Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe and Crane, 1939; Roule and Angel, 1933; Lozano Rey, 1947; Belloc, 1949; Springer and Bullis, 1956; Morrow and Gibbs, 1964; Weitzman, 1967b; Gibbs, 1968; Karnella, 1969; Badcock, 1970; Nielsen, 1974; Parin and Sokolovsky, 1976; Parin et al., 1977; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs, 1986d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Ivanov, 1997; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (between 10ºS and 40ºS, mostly western). Indian (western equatorial; southern subtropical convergence). Pacific (northwestern 40ºN - 45ºN; equatorial central; 31ºN 135ºW).

Leptostomias haplocaulus Regan and Trewavas, 1930

Holotype: 33º 15' N 68º 20' W; ZMUC P201917; "DANA" II 1922, 1341-4

Synonyms: *L. haploclonus* (misspelling); Parin et al., 1977

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Nielsen, 1974; Gibbs, 1984d; Post, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (8ºS 14ºW, 13ºS 9ºW, 34ºS 14ºE). Indian Ocean (7º - 14º S, 60º - 65º E). Pacific (6ºS 120ºW).

Observations: The systematics of the specimens from the Indian and Pacific Oceans referred to this species were considered tentative (Gibbs and Barnett, 1990).

Leptostomias bermudensis Beebe, 1932c

Holotype: 32º 20' N 34º 60' W; USNM 170937; "GLADISFEN" 1931, 1015

Synonyms: *L. bermydensis* (misspelling); Vinnichenko, 1997

References: Beebe, 1932c; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow and Gibbs, 1964; Kukuev, 1982; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997

Global distribution: South Atlantic (6ºS 27ºW).

Observations: see Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Leptostomias gracilis Regan and Trewavas, 1930

Syntypes (3): ZMUC P201994-95; BMNH 1929.7.6.10; "DANA" II 1921, 1162-3, 1160-2

Synonyms: *Melanostomias gracilis*; Fowler, 1936

References: Regan and Trewavas, 1930; Fowler, 1936; Backus et al., 1965; Blache et al., 1970; Craddock and Mead, 1970; Parin et al., 1974; Nielsen, 1974; Kukuev, 1982; Kawaguchi and Moser, 1984; Gibbs, 1986d; Gibbs and Barnett, 1990

Global distribution: South Atlantic (eastern from 10ºS to 35ºS. Pacific (southwestern; northwestern; off Hawaii).

Observations: see Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Leptostomias longibarba Regan and Trewavas, 1930

Syntypes (2): ZMUC P201998; BMNH 1929.7.6.11; "DANA" II 1921, 1171-4; "DANA" 1920, 830

Synonyms: *Melanostomias longibarba*; Fowler, 1936

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Grandperin and Rivaton, 1966; Weitzman, 1967b; Badcock, 1970; Morrow, 1973c; Nielsen, 1974; Gibbs, 1984d; Post, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Moore et al., 2003b

Global distribution: South Atlantic (1º S 28º W).

Observations: Gibbs (1984) refers the species from South Africa but later Gibbs (1986) does not report it for the area. A record from northwestern Pacific, based in Grandperin and Rivaton (1966), needs confirmation. See Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Leptostomias macropogon Norman, 1930

Holotype: from souteastern Atlantic; BMNH; "DISCOVER" 1925

References: Norman, 1930; Gibbs, 1968; Badcock, 1970; Gibbs and Barnett, 1990

Global distribution: South Atlantic (35ºS 10ºW; 40ºS 40ºW).

Observations: see Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Leptostomias analis Regan and Trewavas, 1930

Holotype: 17º 43' N 64º 56' W; ZMUC P201916; "DANA" II 1921, 1192-5

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Nielsen, 1974; Kukuev, 1982; Sutton and Hopkins, 1996; Vinnichenko, 1997

Global distribution: South Atlantic (10ºS 28ºW; 11ºS 11ºW; 23ºS 33ºW).

Observations: see Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Leptostomias leptobolus Regan and Trewavas, 1930

Syntypes (2): ZMUC P201997; BMNH 1929.7.6.12; "DANA" II 1921, 1184-4; 1185-3

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Nielsen, 1974; Kukuev, 1982; Sutton and Hopkins, 1996; Vinnichenko, 1997

Global distribution: South Atlantic (14ºS 27ºW).

Observations: A record from Papua New Guinea (based on Kailola [1987] in FishBase) needs verification. See Gibbs and Barnett (1990) and Chapter 5 about the systematics of this species.

Odontostomias masticopogon Norman, 1930

Holotype: 13º 25' N 18º 22' W; BMNH 1930.1.12.516; "DISCOVER" 1925

References: Norman, 1930; Fowler, 1936; Poll, 1953; Blache, 1962; Blache et al., 1970; Parin and Golovan, 1976; Golovan, 1978; Gibbs and Barnett, 1990

Distribution: South Atlantic (eastern to 11ºS).

Observations: Gibbs and Barnett (1990) state that the only difference between the two *Odontostomias* species is the size of the barbel. Thus *O. masticopogon* may be a variant of *O. micropogon* (see also Chapter 5).

Odontostomias micropogon Norman, 1930

Holotype: from souteastern Atlantic; BMNH; "DISCOVER" 1925

References: Norman, 1930; Fraser-Brunner, 1931; Fowler, 1936; Belloc, 1938; Beebe and Crane, 1939; Poll, 1953; Cadenat, 1961; Blache, 1960; Blache, 1962; Weitzman, 1967b; Blache et al., 1970; Karrer, 1973; Parin and Golovan, 1976; Quéro, 1978 in Maurin et al.; Golovan, 1978; Parin et al., 1978; Kawaguchi and Moser, 1984; Fink, 1985; Lloris, 1986; Gibbs and Barnett, 1990

Distribution: South Atlantic (eastern to 18ºS).

Observations: see note under *O. masticopogon*.

Flagellostomias boureei (Zugmayer, 1913)

Holotype: 38º 55' N 34º 07' W; MOM: 91 1524; "HIRONDELLE" II 1912, 3279

Synonyms: *Eustomias boureei* Zugmayer, 1913; Belloc, 1949; / *F. tyrannus* Parr, 1927; / *Aristostomias uncodentatus* Borodin, 1930 / *Stomiatella D* Roule and Angel, 1930 (part);

References: Zugmayer, 1913; Parr, 1927; Borodin, 1930; Norman, 1930; Regan and Trewavas, 1930; Roule and Angel, 1931; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Belloc, 1949; Koefoed, 1956; Imai, 1957; Blache, 1960**;** Blache, 1962; Morrow and Gibbs, 1964; Grandperrin and Rivaton, 1966; Berry and Perkins, 1967; Weitzman, 1967b; Gibbs, 1968; Quéro, 1969; Badcock, 1970; Blache et al., 1970; Rass, 1971; Geistoerfer et al., 1971; Hulley, 1972; Morrow, 1973c; Clarke, 1974; Parin and Golovan, 1976; Parin et al., 1977; Parin et al., 1978; Gushchin and Kukuev , 1981; Kukuev, 1982; Murdy et al., 1983; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs, 1986d; Swinney et al., 1986; Post, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Kukuev et al., 2000; Moore et al., 2003a; Wienerroither, 2003

Distribution: South Atlantic (to 40ºS: not west between 10ºN and 20º S). Indian (western, one record). Pacific (from off Japan to 4ºS 154ºE; off Australia and New Zealand; Hawaii).

Photonectes gracilis Goode and Bean, 1896

Holotype: 14º 31' N 61º 07' W; MCZ 28033; "BLAKE" 1879, 200

References: Goode and Bean, 1896; Jordan and Evermann, 1896; Parr, 1927; Jordan, Evermann and Clark, 1930; Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Uyeno et al., 1983; Fink, 1985

Global distribution: Indo-Pacific (equatorial). Pacific (19º N 123º E).

Photonectes braueri (Zugmayer, 1913)

Holotype: 39º 19' N 35º 24' W; MOM: 91 1555; "HIRONDELLE" II 1912, 3284

Synonyms: *Melanostomias braueri* Zugmayer, 1913; Belloc, 1949; / *P. ovibarba* Regan and Trewavas, 1930; Fowler, 1936; Bertin, 1940; Nielsen, 1974; / ?*Photonectoides paucidentatus* Koefoed, 1956; / *P. braneri* (misspelling) Vinnichenko, 1997

References: Zugmayer, 1913; Regan and Trewavas, 1930; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Belloc, 1949; Koefoed, 1956; Morrow and Gibbs, 1964; Kotthaus, 1972; Morrow, 1973c; Parin et al., 1974; Nielsen, 1974; Gushchin and Kukuev, 1981; Kukuev, 1982; Uyeno et al., 1983; Gibbs, 1984b; Fink, 1985; Gibbs, 1986d; Post, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Bordes et al., 1999; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (eastern from 18º S to 40º S; western from 26ºS to 39ºS). Indian (10ºS – 34ºS, 60ºE –65ºE). Pacific (east of Australia and New Zealand; one record 18ºS 169ºW).

Observations: Gibbs and Barnett (1990) refer that the South Atlantic population of *P. braueri* may be an undescribed species.

Photonectes dinema Regan and Trewavas, 1930

Syntypes (10): ZMUC P202058; P202059; P202060; P202061; P202062; BMNH 1929.7.6.170; 1929.7.6.171; 1929.7.6.172; "MARGRETHE" 1913, 1031; "DANA 1920, 855-12; "DANA" II 1921, 1156-6; "DANA" II 1922, 1322-8; 1322-27, 1330-3, 1353-7, 1356-2

References: Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Grey, 1955; Morrow and Gibbs, 1964; Backus et al., 1969; Nielsen, 1974; Gibbs, 1984d; Kawaguchi and Moser, 1984; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: North Atlantic endemic.

Photonectes leucospilus Regan and Trewavas, 1930

Syntypes (2): ZMUC P202063; 1929.7.6.173; "DANA" II 1921, 1161-4; "DANA" II 1922, 1358-6

References: Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Koefoed, 1956; Morrow and Gibbs, 1964; Blache et al., 1970; Parin and Andriashev, 1972; Nielsen, 1974; Parin et al., 1974; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (8ºS 14ºW; 16ºS 6ºW; 26ºS 27ºW).

Observations: The record from Hawaii (USNM 214457) needs to be re-evaluated.

Photonectes achirus Regan and Trewavas, 1930

Syntypes (4): ZMUC P202055; P202056; P202057; BMNH 1929.7.6.176a; “MARGRETHE” 1913, 1072b; “DANA” II 1921, 1185-8; “DANA” II 1922, 1285-3, 1284-3

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Sutton and Hopkins, 1996

Global distribution: Pacific (north of Australia; 9º S 143º W; 27ºN 171ºW; off Hawaii).

Observations: According to Clarke (1973) and Gibbs and Barnett (1990) this species may be a synonym of *P. caerulescens*. The *S_db* contains 9 records of the species, despite the statement of Gibbs and Barnett (1990) that only the holotype and the Hawaian record are known.

Photonectes caerulescens Regan and Trewavas, 1930

Holotype: 17º 13' N 64º 58' W; ZMUC P201919; “DANA” II 1922, 1269-4

Synonyms: *Photonectes caeruleus* (misspelling); Parin, 1975

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Karnella, 1969; Rass, 1971; Clarke, 1974; Nielsen, 1974; Parin, 1975; Bekker et al., 1975; Parin et al., 1976; Parin et al., 1977; Gibbs and Barnett, 1990

Global distribution: South Atlantic (18ºS 28ºW). Indian (5ºS 60ºE). Pacific (western equatorial; 1ºN - 4ºS, 150ºW - 158ºW; off Hawaii).

Observations: see note under *P. achirus*.

Photonectes mirabilis Parr, 1927

Holotype: 24º 45' N 76º 21' W; YPM 2077; “PAWNEE” 1927, 27

Synonyms: *P. cornutus* Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow and Gibbs, 1964

References: Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow and Gibbs, 1964; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (western between 30ºS and 35ºS; off South Africa). Indian (western equatorial; off southern India). Pacific (5ºS - 14ºS, 147ºE - 152º E; 0º - 6ºS, 150ºW).

Photonectes phyllopogon Regan and Trewavas, 1930

Holotype: 13º 47' N 61º 26' W; ZMUC P201921; “DANA” II 1921, 1183-7

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Rass, 1971; Nielsen, 1974; Parin et al., 1976; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (2ºS 19ºW). Indian (10ºS 65ºW). Pacific (1 specimen; Gibbs and Barnett, 1990).

Photonectes margarita (Goode and Bean, 1896)

Holotype: 28º 38' N 87º 02' W; USNM 39292; “ALBATROSS“ 1885, 2394

Synonyms: *Echiostoma margarita* Goode and Bean, 1896; Jordan and Evermann, 1896; / *E. margaritum*; Jordan, Evermann and Clark, 1930; / *E. richardi* Zugmayer, 1913; Belloc, 1949; / *P. richardi*; Regan and Trewavas, 1930; Roule and Angel, 1931; Roule and Angel, 1933; Fowler, 1936; / *P. flagellatus* Parr, 1927; Regan and Trewavas, 1930; / *P. intermedius* Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; / *P. monodactylus* Regan and Trewavas, 1930; Fowler, 1936; Nielsen, 1974; / *Eustomias aguayoi* Barbour, 1942; / *P. marginata* (misspelling); Borodin, 1931; / *P. margerita* (misspelling); Vinnichenko, 1997

References: Goode and Bean, 1896; Jordan and Evermann, 1896; Zugmayer, 1913; Parr, 1927; Jordan, Evermann and Clark, 1930; Regan and Trewavas, 1930; Borodin, 1931; Roule and Angel, 1931; Beebe, 1933a; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939;Barbour, 1942; Belloc, 1949; Koefoed, 1956; Aron, 1962; Morrow and Gibbs, 1964; Berry and Perkins, 1967; Weitzman, 1967b; Badcock, 1970; Rass, 1971; Clarke, 1974; Nielsen, 1974; Bekker et al., 1975; Parin and Sokolovsky, 1976; Krueger et al., 1977; Parin et al., 1977; Kukuev, 1982; Murdy et al., 1983; Fink, 1985; Scott and Scott, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (eastern to 22º S, mainly south of 13ºS). Indian (from 1ºN to 12ºS west of 65ºE; 30ºS 49ºE; 32ºS 59ºE). Indo-Pacific (from South China Sea to northeastern Australia). Pacific (8ºN - 7ºS 150ºW); off Hawaii; 32ºN - 40ºN, 121ºW - 142ºW).

Photonectes parvimanus Regan and Trewavas, 1930

Syntypes (10): ZMUC P202071; P202072; P202073; P202074; P202075; P202076; BMNH 1929.7.6.177-178; "MARGRETHE" 1913, 1018b; 1019d; "DANA" 1920, 855-7, 883, 891; "DANA" II 1922, 1365-12, 1358-7

Synonyms: *P. fimbria* Regan and Trewavas, 1930; Fowler, 1936; Grandperrin and Rivaton, 1966; Morrow, 1973c; Clarke, 1974; Nielsen, 1974; Fink, 1985; / *P. bifilifer* Beebe, 1933; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow and Gibbs, 1964; Kukuev, 1982; Vinnichenko, 1997

References: Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Blache, 1960; Blache, 1962; Morrow and Gibbs, 1964; Backus et al., 1965; Grandperrin and Rivaton, 1966; Blache et al., 1970; Morrow, 1973c; Clarke, 1974; Nielsen, 1974; Krueger et al., 1977; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs, 1986d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: South Atlantic (29ºS - 33ºS, 3ºE - 8ºE. Pacific (10ºN - 16ºS, 149ºW - 168ºW; equatorial eastern Pacific, North of Australia, off Hawaii)

Echiostoma barbatum Lowe, 1843

Holotype: 32º N 16 W; off Madeira, position estimated; BMNH 1917.7.14.82; no cruise data

Synonyms: *Hyperchoristus tanneri* Gill, 1884; / *E. tanneri*; Regan and Trewavas, 1930; Norman, 1930; Barnard, 1937; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Thomas, 1953; Springer and Bullis, 1956; Marshall, 1960; King and Iversen, 1962; Grandperrin and Rivaton, 1966; Kawaguchi and Moser, 1984; / *E. calliobarba* Parr, 1934; / *E. ctenobarba* Parr 1927; Regan and Trewavas, 1930; Harvey, 1931; Maul, 1948; / *E. ctenobarba ctenobarba* Parr, 1934; / *E. ctenobarba ramifer* Parr, 1934; / *E. guentheri* Regan and Trewavas, 1930; Fowler, 1936; Maul, 1948

References: Lowe, 1943; Günther, 1964; Goode and Bean, 1879; Jordan and Gilbert, 1882; Gill, 1883; Günther, 1887; Lendenfeld, 1887; Jordan, 1887; Goode and Bean, 1896; Jordan and Evermann, 1896; Brauer, 1906; Pappenheim, 1914; Bigelow and Welsh, 1925; Parr, 1927; Jordan, Evermann and Clark, 1930; Norman, 1930; Regan and Trewavas, 1930; Borodin (part), 1931; Harvey, 1931; Parr, 1934; Fowler, 1936; Gregory and Conrad, 1936; Barnard, 1937; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Maul, 1948; Smith, 1949; Bigelow and Schroeder, 1953; Thomas, 1953; Springer and Bullis, 1956; Marshall, 1960; King and Iversen, 1962; Morrow and Gibbs, 1964; Backus et al., 1965; Grandperrin and Rivaton, 1966; Krueger and Gibbs, 1966; Weitzman, 1967b; Gibbs, 1968; Backus et al., 1969; Karnella, 1969; Blache et al., 1970; Rass, 1971; Hulley, 1972; Kotthaus, 1972; Morrow, 1973c; Clarke, 1974; Bekker et al., 1975; Parin, 1975; Badcock and Merret, 1976; Parin and Sokolovsky, 1976; Parin et al., 1976; Krueger et al., 1977; Parin et al., 1977; Somiya, 1979; Zama and Yasuda, 1979; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs, 1986d; Scott and Scott, 1988; Gibbs and Barnett, 1990; Mesinger and Case, 1990; Smale et al., 1995; Sutton and Hopkins, 1996; Vinnichenko, 1997; Figueroa et al., 1998; Moore et al., 2003a

Global distribution: South Atlantic (to 40º S). Indian (1ºN 60ºE; 21ºS 36ºE; 29ºS 65ºE). Indo-Pacific. Pacific (17ºS 148ºE; off New Zealand; off Japan; 3ºN - 14ºS, 144ºW - 153ºW).

Melanostomias bartonbeani Parr, 1927

Holotype: 44º 10' N 52º 35' W; USNM 22364; "SETH STOCKBRIDGE", 298

Synonyms: *M. spilorhynchus* Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Morrow and Gibbs, 1964; Karnella, 1969; Blache et al., 1970; Quéro, 1970; De Groot and Nijssen, 1971; Morrow, 1973c; Nielsen, 1974; Krefft, 1976; Parin and Golovan, 1976; Parin and Pokhilskaya, 1978; Gushchin and Kukuev, 1981; Kukuev, 1982; Kawaguchi and Moser, 1984; Scott and Scott, 1988; Brooks and Saenger, 1991; Vinnichenko, 1997; Kukuev et al., 2000; / *M. bulbosus* Beebe, 1933a; Beebe, 1937; Mead, 1958

References: Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Mead, 1958; Morrow and Gibbs, 1964; Karnella, 1969; Blache et al., 1970; Quéro, 1970; De Groot and Nijssen, 1971; Morrow, 1973c; Nielsen, 1974; Krefft, 1976; Parin and Golovan, 1976; Parin and Pokhilskaya, 1978; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Gibbs, 1986d; Post, 1988; Gibbs and Barnett, 1990; Brooks and Saenger, 1991; Vinnichenko, 1997; Kukuev et al., 2000; Kukuev, 2002; Kukuev and Trunov, 2002; Sigurðsson et al., 2002; Moore et al., 2003a; Moore et al., 2003b; Wienerroither, 2003; Fock et al., 2004

Global distribution: South Atlantic (between 20ºS and 40ºS). Indian (17ºS - 22ºS, mostly west of 70ºE). Pacific (Gibbs and Barnett, 1990).

Melanostomias biseriatus Regan and Trewavas, 1930

Syntypes (4): 33º 18' N 56º 03' W; ZMUC P202010-12; BMNH 1929.7.6.146; “MARGRETHE” 1913, 1031

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Gibbs, 1960; Morrow and Gibbs, 1964 (part); Backus et al., 1965; Blache et al., 1970; Morrow, 1973c (part); Nielsen, 1974; Uyeno et al., 1983; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (0º 34ºW; 9ºS 27ºW; 21ºS 30ºW).

Observations: Parin and Pokhilskaya (1978) relegated *M. biseriatus* to synonym of *M. melanopogon*; however, Gibbs (1984d) and Gibbs and Barnett (1990) considered that *M. biseriatus* is a valid species. *M. albibarba* was synonymised to *M. biseriatus* by Morrow and Gibbs (1964) and Morrow (1973), but later Gibbs and Barnett (1990) synonymised the *M. albibarba* to *M. melanops*. Parin and Pokhilskaya (1978) referred that many *M. melanops* were classified previously as *M. biseriatus*, as it was recognised by Gibbs (1984d). Several institutions (e.g. USNM) holds lots labelled as *M. biseriatus* from the Indian and Pacific oceans but Gibbs and Barnett (1990) do not refer the species for those oceans; therefore the actual status of those specimens needs to be re-evaluated

Melanostomias macrophotus Regan and Trewavas, 1930

Syntypes (3): ZMUC P202014; BMNH 1929.7.6.151; 1929.7.6.152; “DANA” II 1921, 1184-2; “DANA” II 1922, 1256-4, 1274-5

Synonyms: *M. pauciradius* Matsubara, 1938; Ueno, 1971; Parin and Sokolovsky, 1976; Parin et al., 1977; Parin and Pokhilskaya, 1974; / *M. melanopogon* (non Regan and Trewavas, 1930); Morrow and Gibbs, 1964 (part); Rass, 1971; Morrow, 19731973c (part); / *Melanostomias* sp 2; Parin et al., 1977

References: Regan and Trewavas, 1930; Matsubara, 1938; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Rass, 1971; Ueno, 1971; Morrow, 1973c (part); Nielsen, 1974; Parin and Pokhilskaya, 1974; Parin and Sokolovsky, 1976; Parin et al., 1977; Uyeno et al., 1983; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (28ºS 40ºW). Indo-Pacific (off Sumatra). Pacific (29ºS 175ºW central equatorial; off Hawaii).

Observations: *M. pauciradius* is a name used for the Pacific populations of *M. macrophotus* (Gibbs and Barnett, 1990).

Melanostomias margaritifer Regan and Trewavas, 1930

Syntypes (2): ZMUC P202015; BMNH 1929.7.6.153; “DANA 1921, 950; “DANA” II 1922, 1216-3

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Sutton and Hopkins, 1996

Global distribution: Pacific (off Hawaii).

Melanostomias melanopogon Regan and Trewavas, 1930

Syntypes (4): ZMUC P202016; P202017; P202018; BMNH 1929.7.6.150; “MARGRETHE” 1913, 1063-4; “DANA” II 1922, 1242-7, 1334-3, 1242-6

Synonyms: *M. melanops* (non Brauer, 1902); Parr, 1927 (part)

References: Parr, 1927 (part); Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Blaxter et al., 1971; Morrow, 1973c (part); Nielsen, 1974; Kukuev, 1982; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: North Atlantic endemic.

Melanostomias melanops Brauer, 1902

Holotype: Caught at the off Sumatra; ZMHU?

Synonyms: *M. albibarba* Regan and Trewavas, 1930; Fowler, 1936; Blache, 1960; Cadenat, 1961; King and Iversen, 1962; Nielsen, 1974 / *M. biseriatus* (non Regan and Trewavas, 1930); Morrow and Gibbs, 1964 (part); Rass, 1971; Morrow, 1973c (part); Bekker et al., 1975; Parin, 1975; Parin and Golovan, 1976; Parin and Sokolovsky, 1976; Parin et al., 1976; Parin et al., 1977 (part) / Melanostomias sp 2; Parin et al., 1977); *M. melapos* (misspelling); Vinnichenko, 1997

References: Brauer, 1902; Brauer, 1906; Weber and Beaufort, 1913; Parr (part), 1927; Regan and Trewavas, 1930; Fowler, 1936; Beebe and Crane, 1939; Blache, 1960; Cadenat, 1961; King and Iversen, 1962; Morrow and Gibbs, 1964; Rass, 1971; Morrow, 1973c (part); Nielsen, 1974; Bekker et al., 1975; Parin, 1975; Parin and Golovan, 1976; Parin and Sokolovsky, 1976; Parin et al., 1976; Parin et al., 1977; Parin and Pokhilskaya, 1978; Parin et al., 1978; Kukuev, 1982; Uyeno et al., 1983; Gibbs, 1984d; Gibbs and Barnett, 1990; Mesinger and Case, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: South Atlantic (to 40ºS). Indian (7ºN 60ºE; central and eastern). Pacific (11ºN - 4ºS, 149ºW - 158ºW; 6ºS 152ºE); northwestern to 30ºN; off Hawaii; northeast to 40ºN).

Observations: See note under *M. biseriatus*. Several records of M. biseriatus records from South Atlantic, Indian and Pacific probably refer to this species. Gibbs and Barnett (1990) report two *Melanostomias* sp. similar to *M. melanops*. The group needs to be revised.

Melanostomias tentaculatus Regan and Trewavas, 1930

Syntype (2): ZMUC P201991; BMNH 1929.7.6.136; “DANA, 1920, 858; “DANA” II 1921, 1190

Synonyms: *Haplostomias tentaculatus* Regan and Trewavas, 1930; Smith, 1949 (part) King and Iversen, 1962; Nielsen, 1974; / *H. bituberatus* Regan and Trewavas, 1930; Nielsen, 1974

References: Regan and Trewavas, 1930; Smith, 1949 (part) King and Iversen, 1962; Morrow and Gibbs, 1964; Backus et al., 1965; Weitzman, 1967b; Gibbs, 1968; Backus et al., 1969; Rass, 1971; Morrow, 1973c; Nielsen, 1974; Parin and Golovan, 1976; Parin, 1976; Parin and Sokolovsky, 1976; Parin et al., 1977; Parin and Pokhilskaya, 1978; Kukuev, 1982; Gibbs, 1984d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (to 8ºS; 28ºS - 36ºS. Indian Ocean. Indo-Pacific (South China Sea). Pacific (from ca. 10ºN to New Zealand; off Hawaii).

Melanostomias valdiviae Brauer, 1902

Holotype: From Coast of Sumatra (00º 15' 2" N 98º 08' 08" E); ZMHU 17448

Synonyms: *M. heteropogon* Regan and Trewavas, 1930; Nielsen, 1974; / *M. melanocaulus* Regan and Trewavas, 1930; Nielsen, 1974; / *M. stewarti* Fowler, 1934; / *M. vierecki* Fowler, 1934; / *M. pauciradius* (non Matsubara, 1938); Parin et al., 1977

References: Brauer, 1906; Weber and Beaufort, 1913; Parr, 1927; Regan and Trewavas, 1930; Fowler, 1934; Imai, 1957; Morrow and Gibbs, 1964 (part); Berry and Perkins, 1967; Bradbury et al., 1971; Rass, 1971; Morrow, 1973c; Nielsen, 1974; Parin, 1975; Parin et al., 1976; Parin et al., 1977; Parin and Pokhilskaya, 1978; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Gibbs, 1986d; Post, 1988; Scott and Scott, 1988; Gibbs and Barnett, 1990, Sutton and Hopkins, 1996; Vinnichenko, 1997; Porteiro et al., 1999; Moore et al., 2003a

Global distribution: South Atlantic (western at 10ºS and 18ºS; central and eastern from 26ºS to 39ºS). Indian (24ºS 65ºE to Ceylon). Indo-Pacific. Pacific (from Japan to New Zealand; central equatorial; off Hawaii; 32ºN 121ºW).

Observations: Gibbs and Barnett (1990) considered *M. stewarti* Fowler, 1934 and *M. vierecki* Fowler, 1934 synonyms of this species; however, Harold et al. (1999; and FishBase, after the authors) considered *M. stewarti* and *M. vierecki* valid species, without any comment.

Grammatostomias circularis Morrow, 1959

Holotype: 18º 55' N 66º 10' W; YPM 3773; no cruise data

References: Morrow, 1959; Morrow and Gibbs, 1964; Kukuev, 1982; Gibbs, 1984b; Post, 1988; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: South Atlantic (10ºS 27ºW; 23ºS 33ºW).

Observations: The western Indian record (ZMUC P208916) needs to be studied.

Grammatostomias dentatus Goode and Bean, 1896

Holotype: 38º 19' N 69º 02' W; USNM 37370; “ALBATROSS“ 1885, 2565

Synonyms: *Lamprotoxus angulifer* Beebe, 1932c; Beebe, 1933a; Beebe, 1937; Mead, 1958

References: Goode and Bean, 1896; Jordan and Evermann, 1896; Parr, 1927; Jordan, Evermann and Clark, 1930; Regan and Trewavas, 1930; Beebe, 1932c; Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow, 1959; Morrow and Gibbs, 1964; Krefft, 1974; Fink, 1985; Swinney, 1988a; Gibbs and Barnett, 1990; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: South Atlantic (western between 20ºS and 30ºS). Indian (eastern equatorial). Pacific (3ºS - 7ºS, 150ºE; 14ºS 150ºW).

Grammatostomias flagellibarba Holt and Byrne, 1910

Holotype: 51º 20' N 11º 56' W; BMNH 1910.9.17.2; no cruise data

Synonyms: *Lamprotoxus flagellibarba*; Boulenger, 1913; Holt and Byrne, 1913; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1931; Beebe, 1937; Roule and Angel, 1933; / *L. paucifilis* Regan and Trewavas, 1930; / *L. phanobrochus* Regan and Trewavas, 1930; / *G. paucifilis;* Beebe and Crane, 1939 / *G. phanobrochus;* Beebe and Crane, 1939

References: Holt and Byrne, 1910; Boulenger, 1913; Holt and Byrne, 1913; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1931; Roule and Angel, 1933; Beebe, 1937; Beebe and Crane, 1939; Morrow, 1959; Morrow and Gibbs, 1964; Morrow, 1973c; Kukuev, 1982; Gibbs, 1984b; Fink, 1985; Swinney, 1988a; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: North Atlantic endemic.

Bathophilus altipinnis Beebe, 1933a

Holotype: 32º 12' N 64º 36' W; USNM 170926; “GLADISFEN“ 1929, 214

Synonyms: *Bathophilus* cf. *altipinnis*; Clarke, 1974

References: Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Mead, 1958; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Clarke, 1974; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: Pacific (1ºN 158ºW; off Hawaii).

Bathophilus nigerrimus Giglioli, 1884

Holotype: 38º N 15º 35' E; near Messina, Mediterranean; position estimated; MZUF: 4706;

Synonyms: *Parabathophilus gloriae* Matallanas, 1984

References: Giglioli, 1882; Giglioli, 1884; Günther, 1887; Goode and Bean, 1896; Sicher, 1896; Balducci, 1915; Sanzo, 1915a, b, c; Sanzo, 1918; Parr, 1927; Regan and Trewavas, 1930; Sanzo, 1931; Beebe, 1933a; Fowler, 1936; Beebe and Crane, 1939; Spartà, 1948; Tortonese, 1960; Rimbault, 1963; Tortonese, 1963; Morrow and Gibbs, 1964; Backus et al., 1965; Tortonese and Demir, 1965; Barnett and Gibbs, 1968; Gibbs, 1968; Backus et al., 1969; Berdar, 1970; Rass, 1971; Morrow, 1973c; Parin et al., 1974; Cavaliere and Berdar, 1976; Parin and Sokolovsky, 1976; Quéro, 1978 in Maurin et al.; Parin et al., 1977; Tortonese, 1979; Gibbs, 1984d; Kawaguchi and Moser, 1984; Matallanas, 1984; Gibbs, 1986d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (to 9ºS; 34ºS - 35ºS). Indian. Indo-Pacific (South China Sea). Pacific (Japan; Formosa; Australia; 6ºN 150ºW; off Hawaii).

Observations: According to Morrow and Gibbs (1964) *B. nigerrimus* is a NOMEN NUDUM but Eschmeyer refers the catalogue MZUF 4706.

Bathophilus proximus Regan and Trewavas, 1930

Holotype: 35º 51' N 66º 43' W; ZMUC P201892; “DANA” II 1922, 1353-5

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Bathophilus longipinnis (Pappenheim, 1914)

Holotype: 24º 41' N 32º 21' W; no collection data; “VALDIVIA” D.Südpolar Exp.

Synonyms: *Melanostomias longipinnis* Pappenheim, 1914 / *Gnathostomias longifilis* Pappenheim, 1914 / *Bathophilus longifilis*; Parr, 1927; Fowler, 1936; / cf. *Bathophilus flemingi;* Aron and McCrery, 1958

References: Pappenheim, 1914; Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Craddock and Mead, 1970; Kotthaus, 1972; Clarke, 1974; Parin, 1976; Parin and Sokolovsky, 1976; Gibbs, 1986d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (at 9ºS 7ºE, 11ºS 7ºW; 24ºS - 35ºS, 38ºW - 10ºE). Indian (southwestern). Indo-Pacific. Pacific (off New Zealand; central equatorial; off Hawaii; 31ºN 148ºW; off Samoa; off Chile).

Bathophilus brevis Regan and Trewavas, 1930

Syntypes (3): ZMUC P201935; P201936; BMNH 1929.7.6.20; “DANA” II 1921, 1162-1; “DANA” II 1922, 1368-1, 1341-2

Synonyms: *Notopodichthys brevis*; Fowler, 1936; Blache et al., 1970

References: Regan and Trewavas, 1930; Beebe, 1933a; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Backus et al., 1965; Barnett and Gibbs, 1968; Blache et al., 1970; Craddock and Mead, 1970; Clarke, 1974; Markle and Musick, 1974; Parin and Sokolovsky, 1976; Parin et al., 1977; Kawaguchi and Moser, 1984; Fink, 1985; Swinney, 1988b; Gibbs and Barnett, 1990; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (eastern to 27ºS). Indo-Pacific. Pacific (Japan; New Zealand; off Hawaii; Chile).

Bathophilus pawneei Parr, 1927

Syntypes (3): YPM 2072; 2073; 2074; “PAWNEE” 1927, 5; “PAWNEE” 1927, 7, 23

Synonyms: *B. chironema* Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964 / *B. melas* Regan and Trewavas, 1930; Morrow and Gibbs, 1964

References: Parr, 1927; Norman, 1930; Regan and Trewavas, 1930; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Grey, 1959; Marshall, 1960; Blache, 1960; Blache, 1962; King and Iversen, 1962; Morrow and Gibbs, 1964; Backus et al., 1965; Weitzman, 1967b; Barnett and Gibbs, 1968; Gibbs, 1968; Backus et al., 1969; Karnella, 1969; Blache et al., 1970; Backus et al., 1970; Bradbury et al., 1971; Rass, 1971; Clarke, 1974; Parin et al., 1974; Parin and Sokolovsky, 1976; Parin, 1976; Parin et al., 1977; Parin et al., 1978; Fink, 1985; Swinney, 1988b; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a; Moore et al., 2003b; Wienerroither, 2003

Global distribution: South Atlantic (to 7ºS; 26ºS 37ºW). Indian. Indo- Pacific. Pacific (1º - 10º S, 138º - 152º E; 4ºN 158ºW; off Japan).

Bathophilus digitatus (Welsh, 1923)

Holotype: 32º N 68º W; 225 mi. west of Bermuda; position estimated; USNM 84291; ”GRAMPUS” 1914, 10171

Synonyms: *Dactylostomias digitatus* Welsh, 1923; / *B. longipes* Regan and Trewavas, 1930; Fowler, 1936; Imai, 1957; Morrow and Gibbs, 1964; Badcock, 1970; Rass, 1971; Bekker et al., 1975

References: Welsh, 1923; Parr, 1927; Regan and Trewavas, 1930; Fowler, 1936; Imai, 1957; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Badcock, 1970; Rass, 1971; Morrow, 1973c; Clarke, 1974; Bekker et al., 1975; Gibbs, 1984d; Gibbs, 1986d; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (9ºS 7ºE; 10ºS 30ºW; 26ºS 3ºW). Indian (11ºS 50ºE; off tip of India; equatorial eastern). Indo-Pacific. Pacific (5ºS 152ºW; 18º S 149ºW; Japan; off Hawaii).

Bathophilus schizochirus Regan and Trewavas, 1930

Holotype: 25º 50' N 76º 55' W; ZMUC P201893; "DANA" II 1922, 1239-3

Synonyms: *B. howelli* Barbour, 1942; Morrow and Gibbs, 1964

References: Regan and Trewavas, 1930; Barbour, 1942; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Rass, 1971; Parin and Andriashev, 1972; Clarke, 1974; Parin et al., 1974; Parin et al., 1977; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (5ºS 8ºE, 16ºS 5ºW, 27ºS 37ºW). Indian (North of Madagascar and south of India). Indo-Pacific. Pacific (off Hawaii).

Bathophilus vaillanti (Zugmayer, 1911)

Holotype: 37º 37' N 10º 53' W; MOM: 91 1143; "PRINCESSE ALICE" II 1910, 3024

Synonyms: *Trichostomias vaillanti* Zugmayer, 1911; Belloc, 1949; / *T. metallicus* Welsh, 1923 / *B. metallicus;* Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Grey, 1955; Koefoed, 1956; Marshall, 1960; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Backus et al., 1969; Backus et al., 1970; Badcock, 1970; Kotthaus, 1972; Morrow, 1973c; Quéro, 1978 in Maurin et al.; Kukuev, 1982; Fink, 1985; Vinnichenko, 1997 / *B. havanae* Barbour, 1942; / *B. simplex* Parr, 1927; / *Nasistomias curvatus* Koefoed, 1956 / *T. alberti* Roule and Angel, 1931; Roule and Angel, 1933; Belloc, 1949

References: Zugmayer, 1911; Welsh, 1923; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1931; Beebe, 1933a; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Barbour, 1942; Belloc, 1949; Grey, 1955; Koefoed, 1956; Marshall, 1960; Morrow and Gibbs, 1964; Barnett and Gibbs, 1968; Backus et al., 1969; Backus et al., 1970; Badcock, 1970; Kotthaus, 1972; Morrow, 1973c; Badcock and Merret, 1976; Quéro, 1978 in Maurin et al.; Kukuev, 1982; Gibbs, 1984d; Kawaguchi and Moser, 1984; Fink, 1985; Gibbs and Barnett, 1990; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: North Atlantic endemic.

Observations: Several records from South Atlantic and southwest Pacific (New Zealand) were not considered until further evidences.

Eustomias braueri Zugmayer, 1911

Holotype: 36º 14' N 08º W; MOM: 91 1212; "PRINCESSE ALICE" II 1910, 3045

Synonyms: *E. stigmatopleura* Regan and Trewavas, 1930 / *E. braure (misspelling);* Vinnichenko, 1997

References: Zugmayer, 1911; Regan and Trewavas, 1930; Fowler, 1936; Roule and Angel, 1933; Belloc, 1949; Morrow and Gibbs, 1964; Gibbs, 1971 (report paired fin rays counts and barbel structure); Morrow, 1973c; Parin and Pokhilskaya, 1974; Bekker et al., 1975; Kukuev, 1982; Gibbs et al., 1983; Gibbs, 1984b; Swinney, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997

Global distribution: South Atlantic (8ºS 30ºW; 10ºS 28ºW). Indian (1ºN 98ºE). Indo-Pacific (0ºS, 134ºE). Pacific (19ºN 120ºE; 21ºN - 24ºN, 158ºW; 12ºS 143ºW; 16ºS 150ºW; 3ºN 88ºW).

Eustomias macrurus Regan and Trewavas, 1930

Syntypes (2): ZMUC P201970; BMNH 1929.7.6.74; D-21:912; "MARGRETHE" 1913, 1031

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Grandperrin and Rivaton, 1966; Karnella, 1969; Gibbs, 1971; Parin and Pokhilskaya, 1974; Parin and Sokolovsky, 1976; Kukuev, 1982; Gibbs et al., 1983; Fink, 1985; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Porteiro et al., 1999; Moore et al., 2003a

Global distribution: South Atlantic (8ºS -17ºS, eastern; 15ºS - 30ºS southwest). Indian (36ºS 23ºE; western equatorial; central north; and eastern). Indo-Pacific. Pacific (9ºN – 11ºS west; off Japan; 12ºN – 6ºS, 150ºW - 160ºW; 27ºN 169ºE; off Hawaii).

Eustomias parri Regan and Trewavas, 1930

Holotype: 30º 25' N 44º 46' W; ZMUC P201906; "DANA" II 1922, 1363-1

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Gibbs, 1971; Parin and Pokhilskaya, 1974; Kukuev, 1982; Gibbs et al., 1983; Vinnichenko, 1997

Global distribution: North Atlantic endemic.

Eustomias enbarbatus Welsh, 1923

Holotype: 32º 30' N 68º 25' W; 185 miles W of Bermuda; position estimated; USNM 84282; "GRAMPUS" 1914, 10173

Synonyms: *E. acinosus* Regan and Trewavas, 1930, Morrow and Gibbs, 1964; Blache et al., 1970; Parin et al., 1974; Parin and Pokhilskaya, 1974; / *E. botrypogon* Regan and Trewavas, 1930; Fowler, 1936; Nielsen, 1974 / *E. barbuva* Regan and Trewavas, 1930; Nielsen, 1974; Parin, 1976 / *E. brevifilis* Regan and Trewavas, 1930; Fowler, 1936; King and Iversen, 1962; Nielsen, 1974 / *E. obscurus* Grey, 1955 / *E. regani* Norman, 1930; Fowler, 1936; Blache, 1962

References: Welsh, 1923; Parr, 1927; Norman, 1930; Regan and Trewavas, 1930; Fowler, 1936; Grey, 1955; Blache, 1962; King and Iversen, 1962; Morrow and Gibbs, 1964; Gibbs, 1968; Blache et al., 1970; Gibbs, 1971; Parin and Andriashev, 1972; Gibbs and Craddock, 1973; Parin et al., 1974; Parin and Pokhilskaya, 1974; Nielsen, 1974; Parin et al., 1976; Parin et al., 1977; Zama and Yasuda, 1979; Gibbs et al., 1983; Gibbs and Barnett, 1990; Swinney, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (eastern to 22º S; western to 40º S. Indian (32ºS - 13ºS, 49ºE - 65ºE; 2ºN 73ºE; eastern). Indo-Pacific. Pacific (14ºN – 7ºS, 149ºW - 158ºW; off Hawaii; 27ºS 175ºE).

Eustomias simplex Regan and Trewavas, 1930

Syntypes (3): ZMUC P201974; P201975; BMNH 1929.7.6.108; "MARGRETHE" 1913, 1043-6, 1072; "DANA" II 1922, 1352-1

References: Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Grandperrin and Rivaton, 1966; Gibbs, 1971; Gibbs and Craddock, 1973; Parin and Pokhilskaya, 1974; Nielsen, 1974; Parin et al., 1977; Gibbs et al., 1983; Gibbs, 1984b; Gibbs and Barnett, 1990; Swinney, 1990; Wienerroither, 2003

Global distribution: South Atlantic (west between 5ºS and 23ºS). Indian (eastern, one record). Indo-Pacific (one record).

Eustomias filifer (Gilchrist, 1906)

Holotype: from ENE 36.5 mi off Cape Point, South Africa; Type lost

Synonyms: *Neostomias filiferum* Gilchrist, 1906; Barnard, 1925; / *E. filiferum;* Parr, 1927; Fowler, 1936; Smith, 1949 / *E. ramulosus* Regan and Trewavas, 1930 (part); Nielsen, 1974

References: Gilchrist, 1906; Parr, 1927; Regan and Trewavas, 1930; Barnard, 1925; Fowler, 1936; Barnard, 1937; Smith, 1949; Morrow and Gibbs, 1964; Badcock, 1970; Gibbs, 1971; Kukuev, 1982; Gibbs et al., 1983; Gibbs, 1984d; Gibbs, 1986d; Gibbs, 1986e; Gibbs and Barnett, 1990; Swinney, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (24ºS 0ºE; 21ºS 2ºW; off South Africa; 12ºS to 32ºS west of 27ºW).

Observations:

Eustomias monodactylus Regan and Trewavas, 1930

Syntypes (2): ZMUC P201972; BMNH 1929.7.6.133; "DANA" II 1921, 1158-3, 1166

Synonyms: *E. filifer* (non Regan and Trewavas, 1930); Morrow and Gibbs, 1964 (part); Gibbs et al., 1983 (part); Gibbs and Barnett, 1990 (part)

References: Regan and Trewavas, 1930; Fowler, 1936; Lozano Rey, 1947; Morrow and Gibbs, 1964; Nielsen, 1974; Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990; Swinney, 1990

Global distribution: North Atlantic endemic.

Observations: Morrow and Gibbs (1964) and Gibbs et al. (1983) considered *E. monodactylus* a synonym of *E. filifer*; later Gibbs (1986e) recognized the validity of the species without any comments; Gibbs and Barnett (1990) again synonymised both species. According to R.H. Gibbs notes inside several lots (e.g. USNM 323066; ISH/ZMH 306-1966) E. monodactylus is a valid species. Sutton and Hartel (2004) validated the observations.

Eustomias tetranema Zugmayer, 1913

Holotype: 31º 45' N 20º 17' W; MOM: 91 1450; HIRONDELLE II 1912, 3202

Synonyms: *Parastomias tetranema;* Roule and Angel, 1931; Roule and Angel, 1933;

References: Zugmayer, 1913; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1931; Roule and Angel, 1933; Fowler, 1936; Belloc, 1949; Morrow and Gibbs, 1964; Badcock, 1970; Morrow, 1973c; Kukuev, 1982; Gibbs et al., 1983; Gibbs, 1984b; Gibbs and Barnett, 1990; Swinney, 1990; Vinnichenko, 1997; Wienerroither, 2003

Global distribution: South Atlantic (18º S 29ºW).

Eustomias decoratus Gibbs, 1971

Holotype: 32º 19' N 63º 37' W; USNM 205494; "SANDS" 1969, 6-17P

References: Gibbs, 1971; Parin and Pokhilskaya, 1974; Gibbs et al., 1983

Global distribution: North Atlantic endemic.

Eustomias drechseli Regan and Trewavas, 1930

Holotype: 33º 42' N 36º 16' W; ZMUC P201897; "DANA" II 1922, 1367-1

References: Regan and Trewavas, 1930; Fowler, 1936; Morrow and Gibbs, 1964

Global distribution: North Atlantic endemic.

Observations: the holotype is the only known speciemen.

Eustomias furcifer Regan and Trewavas, 1930

Holotype: 34º 00' N 70º 01' W; ZMUC P201898; "DANA" II 1922, 1342-3

Reference: Regan and Trewavas, 1930; Fowler, 1936; Morrow and Gibbs, 1964; Morrow, 1973c; Nielsen, 1974; Gibbs et al., 1983; Gibbs and Barnett, 1990

Global distribution: South Atlantic (13ºS 09ºW; 29ºS 42º W; 40ºS 44ºW; 40ºS 31ºW). Indian (1ºS 62ºE). Pacific (7ºS 150º W; off Hawaii; 26ºN 172ºW).

Eustomias radicifilis Borodin, 1930

Holotype: 33º N 64º W; MCZ 32268; "ATLANTIS" 1929, 322

References: Borodin, 1930; Gibbs, 1971; Parin and Pokhilskaya, 1974; Kukuev, 1982; Gibbs et al., 1983; Vinnichenko, 1997

Global distribution: North Atlantic endemic.

Eustomias tenisoni Regan and Trewavas, 1930

Holotype: 26º 37' N 54º 45' W; ZMUC P201911; "DANA" II 1922, 1330-4

References: Regan and Trewavas, 1930; Gibbs, 1960; Morrow and Gibbs, 1964; Parin and Pokhilskaya, 1974; Nielsen, 1974; Gibbs et al., 1983; Gibbs and Barnett, 1990

Global distribution: South Atlantic (a doubtful record at 13º S 9º W; southwest 15ºS to 21ºS).

Observations: The Pacific record (of Grandperrin and Rivaton, 1966) needs confirmation (Gibbs and Barnett, 1990).

Eustomias obscurus Vaillant, 1888

Holotype: 36º 11' N 32º 01' W; MNHN: 1885 0064; " TALISMAN" 1883, 119

Synonyms: *E. macrorhynchus* Pappenheim, 1914; Parr, 1927; Fowler, 1936 / *E. proximus* Welsh, 1923; Parr, 1927 / ? *E. zugmayeri* Parr, 1927 / *Pareustomias chabanaudi* Bailly, 1930 / *E. chabanaudi*; Fowler, 1936; / *E. obscura*; Fink, 1985

References: Vaillant, 1888; Goode and Bean, 1896; Zugmayer, 1911; Murray and Hjort, 1912; Pappenheim, 1914; Welsh, 1923; Parr, 1927; Bailly, 1930; Norman, 1930; Regan and Trewavas, 1930; Roule and Angel, 1933; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Bertin, 1940; Lozano Rey, 1947; Koefoed, 1956; Marshall, 1960; Blache, 1962; Morrow and Gibbs, 1964; Backus et al., 1965; Backus et al., 1969; Karnella, 1969; Quéro, 1969; Backus et al., 1970; Badcock, 1970; Blache et al., 1970; Gibbs, 1971; Rass, 1971; Kotthaus, 1972; Parin and Andriashev, 1972; Gibbs and Craddock, 1973; Morrow, 1973c; Parin et al., 1974; Quéro, 1978 in Maurin et al.; Kukuev, 1982; Gibbs et al., 1983; Gibbs, 1984b; Fink, 1985; Gibbs and Barnett, 1990; Swinney, 1990; Vinnichenko, 1997; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (8ºS to 30ºS)

Observations: Sutton and Hopkins (1996a) refer to *E.* cf. *chabanaudi*.

Eustomias bibulbosus Parr, 1927

Holotype: 25º 58' N 77º 26' W; YPM 2039; “PAWNEE” 1927, 11

Synonyms: *E. bibulbosus bibulbosus* Parr, 1927 / E. *bibulbosuas* (misspelling); Vinnichenko, 1997

References: Parr, 1927; Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939 (part); Grey, 1955; Morrow and Gibbs, 1964 (part); Blache et al., 1970; Gibbs, 1971; Gibbs and Craddock, 1973; Gibbs et al., 1983; Gibbs, 1986e; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a

Global distribution: North Atlantic endemic.

Eustomias bituberatus Regan and Trewavas, 1930

Lectotype: 14º 38' N 61º 16' W; ZMUC P201953; “DANA” II 1922, 1284-3;

Synonyms: *E. bibulbosus* Parr, 1927; Morrow and Gibbs, 1964 (part); Blache et al., 1970 (part)

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Blache et al., 1970; Gibbs et al., 1983; Gibbs, 1986e

Global distribution: North Atlantic endemic.

Observations: Gibbs et al. (1983) lectotype is a syntype of Regan and Trwavas,(1930) *E. bituberatus* as three of the six paralectotypes designated.

Eustomias micraster Parr, 1927

Holotype: 24º 51' N 76º 38' W; YPM 2040; “PAWNEE” 1927, 27

Synonyms: *E. bibulbosus micraster* Parr, 1927; / *E. bibulbosus* Parr, 1927 (part); Morrow and Gibbs, 1964 (part: no additional spec.; *E. micraster* in synonym wrongly attributed to Beebe and Crane, 1939); Bekker et al., 1975 (part) / *E. bituberatus* Beebe and Crane, 1939

References: Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Bekker et al., 1975; Gibbs et al, 1983; Gibbs, 1986e; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Eustomias arborifer Parr, 1927

Holotype: 24º 00' N 77º 17' W; YPM 2041; “PAWNEE” 1927, 7

Synonyms: *E. bibulbosus arborifer* Parr, 1927; / *E. bibulbosus*; Beebe and Crane, 1939 (*E. arborifer* in synonymy); Morrow and Gibbs, 1964

References: Parr, 1927; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996

Global distribution: South Atlantic (11ºS 11ºW; to 25ºS west of 27º W).

Eustomias bimargaritatus Regan and Trewavas, 1930

Lectotype: ZMUC P201950; “DANA” II 1922, 1335;

Synonyms: *E. bibulbosus*; Beebe and Crane, 1939 (no additional spec.; *E. bimargaritatus* in synonymy); Morrow and Gibbs, 1964 (reference to *E. bimargaritatus* only); Blache et al., 1970 (part); Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part)

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Blache et al., 1970 (part); Bekker et al., 1975 (part); Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990

Global distribution: North Atlantic endemic.

Observations: The lectotype of Gibbs et al. (1983) is a syntype of Regan and Trewavas's (1930) *E. bimargaritatus* as two of the three paralectotypes designated.

Eustomias kreffti Gibbs, Clarke and Gomon, 1983

Holotype: 04º 34' N 19º 39' W; ISH 2343-1971; "WALTHER HERWIG" CR. 36, 1971, 482-I/ 71

Synonyms: *E. bituberatus* Regan and Trewavas, 1930 (part: the smallest juvenille)

References: Regan and Trewavas, 1930; Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996;

Global distribution: South Atlantic (western to 6ºS).

Eustomias melanonema Regan and Trewavas, 1930

Holotype: 13º 35' N 30º 11' W; ZMUC P201904; "DANA" II 1921, 1162-3

Synonyms: *E. bibulbosus*; Parin et al., 1978; / *E. melanostigma* Regan and Trewavas, 1930 (non type considered *E. melanostigma* by Gibbs et al., 1983); Morrow and Gibbs, 1964 (part: *E. melanonema* in synonymy); Backus et al., 1965; Blache et al., 1970 (part)

References: Regan and Trewavas, 1930; Fowler, 1936, Morrow and Gibbs, 1964; Backus et al., 1965; Blache et al., 1970; Parin et al., 1978; Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990

Global distribution: South Atlantic (to 1ºS).

Eustomias melanostigma Regan and Trewavas, 1930

Lectotype: 17º 43' N 64º 56' W; ZMUC P201971; BMNH 1929.7.6.105; "DANA" II 1922, 1256-4, 1266-4

Synonyms: *E. bibulbosus*; Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part); Parin et al., 1977 (part)

References : Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Backus et al., 1965; Blache et al., 1970; Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part); Parin et al., 1977 (part); Gibbs and Craddock, 1973; Parin and Pokhilskaya, 1974; Gibbs et al., 1983; Gibbs, 1986e; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996;

Global distribution: Indian (North of Madagascar, 3ºN 75ºW). Indo-Pacific (3ºN – 16ºS, 129ºW - 147ºW).

Observations: This is the unique species of the sub-genus *Nominostomias* known to occur in Atlantic and Indo-Pacific (Gibbs et al., 1993). The lectotype and the paralectotype are the Regan and Trewavas's (1930) syntypes.

Eustomias patulus Regan and Trewavas, 1930

Holotype: 26º 15' N 20º 52' W; ZMUC P201907; "DANA" II 1921, 1155-1

References: Regan and Trewavas, 1930; Fowler, 1936; Gibbs et al., 1983; Gibbs and Barnett, 1990;

Global distribution: North Atlantic endemic.

Observations: the holoytype is the only known specimen (Gibb and Barnett, 1990); the western Atlantic specimen UF 227666 needs re-examination.

Eustomias longibarba Parr, 1927

Lectotype: 24º 00' N 77º 17' W; YPM 2037; "PAWNEE" 1927, 7

Synonyms: *E. longibarbus* Parr, 1927; Fowler, 1936 / ?*E. microcephalus* Parr, 1927

References: Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane, 1939; Fowler, 1936; Morrow and Gibbs, 1964 (part); Badcock, 1970; Gibbs, 1971; Rass, 1971; Gibbs and Craddock, 1973; Morrow (part), 1973; Parin and Pokhilskaya, 1974 (part); Bekker at al., 1975; Gibbs et al., 1983; Gibbs, 1984b; Gibbs and Barnett, 1990; Swinney, 1990; Sutton and Hopkins, 1996; Wienerroither, 2003

Global distribution: South Atlantic (western to 10ºS).

Observations: Parr (1927) did not designated a holotype; lectotype by Gibb et al. (1983). Two specimens from southwestern Atlantic (18ºS 28ºW; 23ºS 33ºW) needs to be re-evaluated.

Eustomias bigelowi Welsh, 1923

Holotype: 34 º N 73º W; 170 miles SE of Cape Haterras; position estimated; USNM 84284; ”GRAMPUS” 1914, 10163 1/2

Synonyms: *E. b. bigelowi* Parr, 1927; / *E. b. parvibulbus* Parr, 1927; / *E. parvibulbus;* Regan and Trewavas, 1930; Gibbs and Craddock, 1973; Morrow and Gibbs, 1964 (restor. from synon. of *E. bigelowi*); / *Eustomias* sp. 2; Parin and Pokhilskaya, 1974 (part)

References: Welsh, 1923; Parr, 1927; Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939 (part); Springer and Bullis, 1956; Morrow and Gibbs, 1964 (part); Grandperrin and Rivaton, 1966; Gibbs, 1971 (part); Gibbs and Craddock, 1973; Parin and Pokhilskaya, 1974; Parin and Sokolovsky, 1976; Parin et al., 1977; Gibbs et al., 1983; Clarke, 1987; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Clarke, 2000; Wienerroither, 2003

Global distribution: South Atlantic (eastern to 25ºS). Indian Ocean (southwestern). Pacific (western equatorial; Philippines Sea; central equatorial; off Hawaii; southeastern).

Observations: Parin and Pokhilskaya (1974) and Gibbs et al. (1983) tentatively synonymized *E. triramis* to *E. bigelowi* but Gibbs and Barnett (1990) and Clarke (2000) recuperated *E. triramis* as a valid species.

Eustomias binghami Parr, 1927

Holotype: 22º 31' N 74º 26' W; YPM 2043; “PAWNEE” 1927, 41

Synonyms: *E. frondosus* Regan and Trewavas, 1930; Beebe, 1937

References: Parr, 1927; Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Gibbs, 1971; Morrow, 1973cc (part); Parin and Pokhilskaya, 1974; Gibbs et al., 1983; Fink, 1985; Clarke, 2000

Global distribution: North Atlantic endemic.

Eustomias borealis Clarke, 2000

Holotype: 32º 13' N 64º 16' W; USNM 261281; ”DELAWARE” II 1971, 83N

Synonyms: *E. bigelowi*; Beebe and Crane, 1939 (part); Grey, 1955; Morrow and Gibbs, 1964 (part); / *E. paucifilis;* Beebe, 1937 (part)

References: Beebe, 1937; Beebe and Crane, 1939 (part); Grey, 1955; Morrow and Gibbs, 1964 (part); Clarke, 2000; Moore et al., 2003a

Global distribution: North Atlantic endemic.

Eustomias fissibarbis (Pappenheim, 1914)

Holotype: 24º 41' N 32º 21' W; no collection reported; no cruise data

Synonyms: *Neostomias fissibarbis* Pappenheim, 1914; / *E. nigrifilis* Parr, 1927

References: Pappenheim, 1914; Parr, 1927; Regan and Trewavas, 1930; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Gibbs, 1971; Rass, 1971; Parin et al., 1974; Parin and Pokhilskaya, 1974; Bekker et al., 1975; Parin, 1976; Parin et al., 1977; Gibbs et al., 1983; Scott and Scott, 1988; Gibbs and Barnett, 1990; Sutton and Hopkins, 1996; Clarke, 2000; Moore et al., 2003a

Global distribution: South Atlantic (mostly western to 27ºS). Indian (11ºS 50ºE; 10ºS 64ºE). Indo-Pacific; Pacific (21ºN 150ºE; off Hawaii; 3ºS 145ºW, 14ºS 147W).

Observations: Gibbs (1990) indicates the ZMUH ? collection for holotype.

Eustomias lipochirus Regan and Trewavas, 1930

Holotype: 17º 43' N 64º 56' W; ZMUC P201901; “DANA” II 1922, 1273-2

Synonyms: *E. dactylobolus* Regan and Trewavas, 1930; Fowler, 1936; Nielsen, 1974 / ?*E. melanobolus* Regan and Trewavas, 1930; Fowler, 1936; Nielsen, 1974

References: Regan and Trewavas, 1930; Fowler, 1936; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Blache et al., 1970; Gibbs, 1971; Rass, 1971; Parin and Pokhilskaya, 1978; Nielsen, 1974; Gibbs et al., 1983; Gibbs, 1986c; Gibbs and Barnett, 1990; Swinney, 1990; Smale et al., 1995; Sutton and Hopkins, 1996; Wienerroither, 2003

Global distribution: South Atlantic (14ºS 28ºW; 21ºS 30ºW; 34ºS14ºE. Indian (10ºS 63ºE).

Eustomias macronema Regan and Trewavas, 1930

Holotype: 30º 17' N 20º 44' W; ZMUC P201902; “DANA” II 1921, 1152-5

Synonyms: *E. binghami*; Morrow and Gibbs, 1964 (part); Morrow, 1973c (part)

References: Regan and Trewavas, 1930; Fowler, 1936; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Gibbs, 1971; Morrow, 1973c (part); Nielsen, 1974; Gibbs et al., 1983; Gibbs, 1984b; Gibbs and Barnett, 1990; Swinney, 1990; Clarke, 2000

Global distribution: South Atlantic (21ºS 30ºW; 23ºS 33ºW). Indian (southwestern; south of India; southeast, 18ºS – 20ºS). Indo-Pacific to 13ºS. Pacific (Australia and New Zealand; northwest to 24ºN; central equatorial ; off Hawaii).

Eustomias paucifilis Parr, 1927

Holotype: 23º 58' N 77º 26' W; YPM 2095; “PAWNEE” 1927, 11

Synonyms: *E. bigelowi*; Morrow and Gibbs, 1964; / *E. bigelowi paucifilis* Parr, 1927

References: Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Gibbs et al., 1983; Clarke, 2000

Global distribution: North Atlantic endemic.

Eustomias satterleei Beebe, 1933a

Holotype: 32º 12' N 64º 36' W; USNM 170927; “GLADISFEN“ 1929, 455

Synonyms: *E. silvescens*; Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Clarke, 1982; / *E. bigelowi*?; Parin et al., 1977;

References: Beebe, 1933a; Beebe, 1937; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Parin et al., 1977; Clarke, 1982; Gibbs et al., 1983; Clarke, 1987; Clarke, 2000; Moore et al., 2003a

Global distribution: South Atlantic (18ºS - 20ºS 30ºW). Indian (19ºS 65ºE; 11ºS 50ºE). Indo-Pacific; Pacific (34ºS 152ºE; 15ºS 143ºW; northwestern 17ºN - 23ºN; central equatorial; central north 17ºN - 27ºN).

Eustomias schmidti Regan and Trewavas, 1930

Syntypes (3): ZMUC P201883; P201973; BMNH 1929.7.6.127; “MARGRETHE” 1913, 1019b; “DANA” II 1921, 1178-3; “DANA” II 1922, 1238-1

Synonyms: *E. schidt* (misspelling); Vinnichenko, 1997

References: Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939; Grey, 1955; King and Iversen, 1962; Morrow and Gibbs, 1964; Gibbs, 1971; Rass, 1971; Kotthaus, 1972; Parin et al., 1973; Parin and Pokhilskaya, 1974; Nielsen, 1974; Bekker et al., 1975; Parin, 1976; Krueger et al., 1977; Parin et al., 1977; Parin, 1978; Zama and Yasuda, 1979; Kukuev, 1982; Gibbs et al., 1983; Gibbs, 1984d; Gibbs, 1986d; Gibbs and Barnett, 1990; Swinney, 1990; Smale et al., 1995; Sutton and Hopkins, 1996; Vinnichenko, 1997; Clarke, 2000; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (21ºS - 34ºS). Pacific (eastern Australia 18ºS - 36ºS to New Zealand; northwestern from 23ºN - 31ºN to Japan; 11ºN - 3ºS and 144ºW - 158ºW; off Hawaii; 31ºN 135ºW).

Eustomias silvescens Regan and Trewavas, 1930

Holotype: 17º 45' N 64º 55' W; ZMUC P201910; “DANA” II 1922, 1266

References: Regan and Trewavas, 1930; Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Gibbs, 1971; Gibbs et al., 1983; Clarke, 2000

Global distribution: North Atlantic endemic.

Eustomias triramis Regan and Trewavas, 1930

Holotype: 21º 47' N 47º 11' W; ZMUC P201912; "MARGRETHE" 1913, 1063-4

Synonyms: *E. bigelowi* (non Welsh, 1923); Beebe and Crane, 1939; Morrow and Gibbs, 1964; Parin and Pokhilskaya, 1974 (tentatively); Gibbs et al., 1983 (tentatively)

References: Regan and Trewavas, 1930; Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Parin and Pokhilskaya, 1974 (part); Nielsen, 1974; Gibbs et al., 1983; Gibbs and Barnett, 1990; Clarke, 2000

Global distribution: North Atlantic endemic.

Eustomias dendriticus Regan and Trewavas, 1930

Holotype: 29º 42' N 48º 08' W; ZMUC P201896; "MARGRETHE" 1913, 1058-4

References: Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964 (part); Rass, 1971; Nielsen, 1974; Gibbs et al., 1983 (part); Gibbs and Barnett, 1990 (part); Sutton and Hopkins, 1996; Clarke, 1999

Global distribution: North Atlantic endemic.

Eustomias lanceolatus Clarke, 1999

Holotype: 10º 52' N 22º 09' W; ISH 2616-1971; "WALTHER HERWIG" 1971, 490-II/ 71

References: Clarke, 1999

Global distribution: South Atlantic (2ºS 19ºW).

Eustomias monoclonoides Clarke, 1999

Holotype: 1º 42' N 07º 51' E; ZMUC P208796; "GALATHEA" 1950, 52

Synonyms: *E. dendriticus*; Parin et al., 1978

References: Parin et al., 1978; Clarke, 1999

Global distribution: South Atlantic (1ºS 6ºE).

Eustomias monoclonus Regan and Trewavas, 1930

Holotype: 17º 54' N 64º 54' W; ZMUC P201905; "DANA" II 1921, 1186-4

Synonyms: *E. dendriticus*; Morrow and Gibbs, 1964 (part); Parin and Pokhilskaya, 1974; Gibbs and Barnett, 1990 (part)

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964 (part); Nielsen, 1974; Parin and Pokhilskaya, 1974; Gibbs et al., 1983 (part); Gibbs and Barnett, 1990 (part); Clarke, 1999

Global distribution: South Atlantic (1ºS 6ºE). Indian (12ºS 50ºE 6ºN 92ºE). Indo-Pacific (8ºN 121ºE; 1ºN 136ºE).

Eustomias achirus Parin and Borodulina, 1974

Holotype: Type from Coral Sea (about 15ºS 150ºE)

References: Parin and Pokhilskaya, 1974; Kukuev, 1982; Gibbs et al., 1983; Gibbs and Barnett, 1990; Vinnichenko, 1997; Clarke, 1998; Moore et al., 2003a

Global distribution: Coral Sea.

Observations: The holotype is the only non-North Atlantic specimen. Clarke (1998) mentioned that the specimens from the Atlantic differ from the holotype caught at Coral Sea in several morphologic characters. The specimen reported by Parin and Pokhilskaya (1974) from the western equatorial Pacific and Parin et al. (1977) were considered by Clarke (1998) as *Eustomias* spp.

Eustomias aequatorialis Clarke, 1998

Holotype: Type from SE Atlantic

References: Clarke, 1998

Global distribution: South Atlantic (1ºS 26ºW).

Eustomias insularum Clarke, 1998

Holotype: 16º 08' N 22º 22' W; ISH 525-1968; “WALTHER HERWIG”, 1968, 11-III/ 68

References: Clarke, 1998

Global distribution: North Atlantic endemic.

Eustomias intermedius Clarke, 1998

Holotype: Type from SE Atlantic

References: Clarke, 1998

Global distribution: South Atlantic (8ºS 14ºW).

Eustomias globulifer Regan and Trewavas, 1930

Holotype: 14º 38' N 61º 16' W; ZMUC P201899; “DANA” II 1922, 1285-2

References: Regan and Trewavas, 1930; Gomon and Gibbs, 1985

Observations: a doubtful species according to Gomon and Gibbs (1985); it is only known from the holotype, which is a juvenile with a damaged barbel.

Eustomias brevibarbatus Parr, 1927

Holotype: 23º 55' N 77º 09' W; YPM 2034; “PAWNEE” 1927, 9

References: Parr, 1927; Regan and Trewavas, 1930; Bertin, 1940; Morrow and Gibbs, 1964; Karnella, 1969; Rass, 1971; Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part); Murdy et al., 1983; Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: South Atlantic (western part from the equator to 23ºS 30ºW).

Eustomias contiguus Gomon and Gibbs, 1985

Holotype: 34º 21' N 35º 22' W; ISH 3304-1979; “ANTON DOHRN”, 1979, 340/ 79

References: Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Eustomias dispar Gomon and Gibbs, 1985

Holotype: 08º 57' N 46º 29' W; USNM 222183; ”ATLANTIS” II 1978, RHB2940

References: Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Observations: the holotype is the only specimen known.

Eustomias hypopsilus Gomon and Gibbs, 1985

Holotype: 27º 00' N 86º 00' W; USNM 223639; COLUMBUS ISELIN 1975, 217AF

References: Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Eustomias variabilis Regan and Trewavas, 1930

Lectotype: 14º 38' N 61º 16' W; ZMUC P201984; “DANA” II 1922, 1284-3

Synonyms: *E. trituberatus* Regan and Trewavas, 1930; Nielsen, 1974 / *E. brevibarbatus*; Morrow and Gibbs, 1964 (part); Rass, 1971; Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part)

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964 (part) Rass, 1971; Nielsen, 1974; Parin and Pokhilskaya, 1974 (part); Bekker et al., 1975 (part); Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Observations: Regan and Trewavas (1930) used 17 syntypes to describe *E. variabilis* then Gomon and Gibbs (1985) designated 1 lectoype and 14 paralectotypes.

Eustomias digitatus Gomon and Gibbs, 1985

Holotype: 17º 43' N 64º 56' W; ZMUC P201850; "DANA" II 1922, 1273-7

Synonyms: *E. dubius* Regan and Trewavas, 1930 (part); Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part)

References: Regan and Trewavas, 1930 (part); Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Eustomias dubius Parr, 1927

Holotype: 23º 58' N 77º 26' W; YPM 2036; "PAWNEE" 1927, 11

References: Parr, 1927; Regan and Trewavas (part); Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Rass, 1971; Kukuev, 1982; Gibbs et al., 1983; Gomon and Gibbs, 1985; Vinnichenko, 1997

Global distribution: North Atlantic endemic.

Eustomias polyaster Parr, 1927

Holotype: 22º 31' N 74º 26' W; YPM 2042; "PAWNEE" 1927, 41

References: Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Rass, 1971; Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Eustomias schiffi Beebe, 1932c

Holotype: 32º N 64º W; USNM 170935; "GLADISFEN", 1930, 646

Synonyms: *E. dubius* Beebe and Crane, 1939 (part); Morrow and Gibbs, 1964 (part); Gibbs, 1971

References: Beebe, 1932c; Beebe, 1937; Beebe and Crane, 1939 (part); Mead, 1958; Morrow and Gibbs, 1964 (part); Gibbs, 1971; Gomon and Gibbs, 1985; Moore et al., 2003a

Global distribution: North Atlantic endemic.

Eustomias hulleyi Gomon and Gibbs, 1985

Holotype: 23º 46' N 58º 59' W; ISH 3295-1979; "ANTON DOHRN" 1979, 98/ 79

References: Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Eustomias leptobolus Regan and Trewavas, 1930

Holotype: 23º 13' N 82º 21' W; ZMUC P201900; "DANA" II 1922, 1230-4

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964; Rass, 1971; Nielsen, 1974; Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Eustomias macrophthalmus Parr, 1927

Holotype: 22º 31' N 74º 26' W; YPM 2035; "PAWNEE" 1927, 41

References: Parr, 1927; Regan and Trewavas, 1930; Beebe and Crane, 1939; Morrow and Gibbs, 1964; Rass, 1971; Parin and Pokhilskaya, 1974; Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Eustomias precarius Gomon and Gibbs, 1985

Holotype: 19º 21' N 65º 39' W; USNM 259636; PILLSBURY 1969, 828

References: Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Eustomias pyrifer Regan and Trewavas, 1930

Holotype: 17º 59' N 64º 41' W; ZMUC P201908; "DANA" II 1921, 1186-9

Synonyms: *E. xenobolus*; Morrow and Gibbs, 1964 (part)

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964 (part); Nielsen, 1974; Gibbs et al., 1983; Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Observations: only the holotype is known.

Eustomias quadrifilis Gomon and Gibbs, 1985

Holotype: 38º 58' N 71º 16' W; USNM 266296; "OCEANUS" 1982, MOC20-010,4

References: Gomon and Gibbs, 1985

Global distribution: North Atlantic endemic.

Observations: only the holotype is known.

Eustomias xenobolus Regan and Trewavas, 1930

Holotype: 17º 43' N 64º 56' W; ZMUC P201913; "DANA" II 1922, 1279-1

References: Regan and Trewavas, 1930; Morrow and Gibbs, 1964 (part); Rass, 1971; Nielsen, 1974; Parin and Pokhilskaya, 1974; Gibbs et al., 1983; Gomon and Gibbs, 1985; Sutton and Hopkins, 1996

Global distribution: North Atlantic endemic.

Idiacanthus fasciola Peters, 1877

Syntypes: N of Australia at 117º E and 01º 04' N 136º 03' E; deposition unknown.

Synonyms: *Bathyophis ferox* Günther, 1878; / *Idiacanthus ferox;* Günther, 1887; Murray and Hjort, 1912*; / Stylophthalmus paradoxus* (part) Brauer, 1902

References: Peters, 1877; Günther, 1878; Günther, 1887; Brauer, 1906; Brauer, 1908; Murray and Hjort, 1912; Bierbaum, 1914; Parr, 1927; Regan and Trewavas, 1930; Beebe, 1933b; Roule and Angel, 1933; Beebe, 1934; Koefoed, 1956; Briggs, 1960; Nicol, 1960; Gibbs, 1964b; Backus et al., 1965; Novikova, 1967; Weitzman, 1967b; Backus et al., 1969; Karnella, 1969; Backus et al., 1970; Badcock, 1970; Bradbury et al., 1971; Hulley, 1972; Kotthaus, 1972; Krueger, 1973; Krefft, 1974; Bekker et al., 1975; Badcock and Merret, 1976; Parin et al., 1977; Quéro, 1978 in Maurin et al.; Gushchin and Kukuev , 1981; Weihs and Moser, 1981; Kukuev, 1982; Murdy et al., 1983; Gibbs, 1984f; Kawaguchi and Moser, 1984; Fink, 1985; Hulley, 1986; Scott and Scott, 1988; Krueger, 1990; Smale et al., 1995; Sutton and Hopkins, 1996; Vinnichenko, 1997; Wagner et al., 1998; Bordes et al., 1999; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (26ºS - 36ºS). Indian (north of 23ºS). Indo-Pacific. Pacific (western and central between 23ºS and 27ºN).

Aristostomias lunifer Regan and Trewavas, 1930

Syntypes (4): ZMUC P20425; P20426; P201925; BMNH 1929.7.6.249; "DANA" II 1922, 1195-2, 1291-1, 1320-2, 1352-1

Synonyms: *A. photodactylus* Beebe, 1933; Mead, 1958; Morrow, 1964c; Parin et al., 1976; Parin et al., 1978; / *A. scintillans* (non Gilbert, 1915); Parr, 1927

References: Regan and Trewavas, 1930; Parr, 1927; Beebe, 1933; Mead, 1958; Backus et al., 1969; Morrow, 1964c; Goodyear, 1973; Clarke, 1974; Nielsen, 1974; Parin et al., 1976; Parin et al., 1977; Parin et al., 1978; Goodyear, 1980; Kukuev, 1982; Gibbs, 1984e; Fink, 1985; Goodyear and Gibbs, 1986; Goodyear, 1990; Sutton and Hopkins, 1996; Vinnichenko, 1997; Bordes et al., 1999; Moore et al., 2003a

Global distribution: South Atlantic (off Brazil; 30ºS 3ºW). Indian (from tip of India southeastward to 10ºS). Indo-Pacific. Pacific (18ºS 149ºE; 20ºS 177ºW; central equatorial; off Hawaii and northward to 28ºN).

Aristostomias tittmanni Welsh, 1923

Holotype: 35º N 73º W; USNM 84290; GRP-14:10161; Position estmated (115 mi. E of Cape Haterras)

Synonyms: *A. grimaldii* (non Zugmayer, 1913); Parr, 1927 (part);

References: Welsh, 1923; Parr, 1927; Regan and Trewavas, 1930; Fowler, 1936; Beebe, 1937; Morrow, 1964c; Backus et al., 1965; Backus et al., 1969; Karnella, 1969; Goodyear, 1973; Krueger et al., 1977; Goodyear, 1980; Kukuev, 1982; Gibbs, 1984e; Fink, 1985; Post, 1988; Scott and Scott, 1988; Sutton and Hopkins, 1996; Vinnichenko, 1997; Moore et al., 2003a; Moore et al., 2003b

Global distribution: South Atlantic (to 10ºS). Indian (southwestern from 0º to 20ºS; eastern from 5ºS to 10ºN). Pacific (central from 20ºN to 10ºS; off Chile).

Observations: If *A. ponticus* (an unpublished species described by Goodyear [1980]) is a different species, *A. tittmanni* is a North Atlantic endemic species. The specimens named by *A. ponticus* are those occurring in the equatorial waters and southeastern Caribbean (e.g. Backus et al., 1965; Clarke, 1974 after Goodyear, 1980).

Aristostomias grimaldii Zugmayer, 1913

Holotype: 30º 46' N 25º 47' W; MOM: 91 1505; ”HIRONDELLE” II 1912, 3222

References: Zugmayer, 1913; Welsh, 1923; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1933; Fowler, 1936; Belloc, 1949; Morrow, 1964c; Goodyear, 1973; Clarke, 1974; Bekker et al., 1975; Badcock and Merret, 1976; Parin et al., 1977; Goodyear, 1980; Uyeno et al., 1983; Gibbs, 1984e; Campbell. and Herring, 1987; Bowmaker et al., 1988; Goodyear, 1990; Sutton and Hopkins, 1996; Porteiro et al., 1999; Moore et al., 2003a; Wienerroither, 2003

Global distribution: South Atlantic (0ºS 35ºW; 35ºS 49ºW). Indian (central at 15ºS). Indo-Pacific. Pacific (off Hawaii and westward to 170ºE).

Aristostomias xenostoma Regan and Trewavas, 1930

Syntypes (16): ZMUC P20438; P20439; P20440; P20441; P20442; P20443; P20444; P20445; P20446; P20447; P20448; P201927; BMNH 1929.7.6.244; 1929.7.6.245; 1929.7.6.246; 1929.7.6.247; “DANA” II 1921, 1162-1, 1162-3, 1163-3, 1166-2, 1171-9, 1171-12, 1178-3, 1181-3, 1181-4, 1183-7, 1184-3; “DANA” II 1922, 1228, 1280-4, 1285-1

References: Regan and Trewavas, 1930; Norman, 1930; Fowler, 1936; Bertin, 1940; Morrow, 1964c; Karnella, 1969; Parin et al., 1973; Nielsen, 1974; Parin, 1974; Parin et al., 1974; Badcock and Merret, 1976; Parin et al., 1976; Parin et al., 1977; Goodyear, 1980; Fink, 1985; Goodyear, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (to 8ºS). Indian (southwest north of 20ºS to Indo-Pacific. Pacific (northeast Australia to 15ºS; 10ºS – 10ºN, 120ºW – 160ºW).

Aristostomias polydactylus Regan and Trewavas, 1930

Syntypes (11): ZMUC P20427; P20428; P20429; P20430-31; P20432; P201926; BMNH 1929.7.6.256; 1929.7.6.257; 1929.7.6.258; 1929.7.6.259; “DANA” 1921, 927b, 927c, 928; “DANA” II 1921, 1189-4, 1190-6, 1194-4; “DANA” II 1922, 1217-5, 1223-4, 1228, 1239

References: Regan and Trewavas, 1930; Morrow, 1964c; Karnella, 1969; Clarke, 1974; Nielsen, 1974; Bekker et al., 1975; Parin 1976; Krueger et al., 1977; Parin et al., 1977; Goodyear, 1980; Goodyear, 1990; Sutton and Hopkins, 1996; Moore et al., 2003a

Global distribution: South Atlantic (to South Africa). Indian (5ºN-20ºS). Indo-Pacific. Pacific (southwestern to New Zealand; northwest to ca. 20ºN; central from Hawaii to 10ºS).

Malacosteus niger Ayres, 1848

Holotype: 42º N 50º W; Type lost; no reference to collection

Synonyms: *M. indicus* Günther, 1878; Lendenfeld, 1887; Günther, 1887; Alcock, 1889; Goode and Bean, 1896; Brauer, 1906; Brauer, 1908; Zugmayer, 1911; Murray and Hjort, 1912; Weber and Beaufort, 1913; Bierbaum, 1914; Regan and Trewavas, 1930; Maul, 1948; Smith, 1949; Morrow, 1964c; McAllister, 1967; O'Day and Fernández, 1974 / *M. choristodactylus* Vaillant, 1888; Goode and Bean, 1896; Murray and Hjort, 1912; Bertin, 1940; Morrow, 1964c / *M. danae* Regan and Trewavas, 1930; Morrow, 1964c; Nielsen, 1974

References: Ayres, 1848; Ayres, 1849; Günther, 1864; Günther, 1878; Goode and Bean, 1879; Jordan and Gilbert, 1882; Jordan, 1887; Lendenfeld, 1887; Günther, 1887; Vaillant, 1888; Alcock, 1889; Goode and Bean, 1896; Jordan and Evermann, 1896; Jordan and Evermann, 1900; Brauer, 1906; Brauer, 1908; Zugmayer, 1911; Murray and Hjort, 1912; Weber and Beaufort, 1913; Bierbaum, 1914; Jordan, 1919; Roule, 1919; Parr, 1927; Beebe, 1929; Jordan, Evermann and Clark, 1930; Norman, 1930; Regan and Trewavas, 1930; Roule and Angel, 1930; Borodin, 1931; Roule and Angel, 1933; Parr, 1934; Fowler, 1936; Beebe, 1937; Bertin, 1940; Norman, 1939; Bertin, 1940; Lozano Rey, 1947; Maul, 1948; Smith, 1949; Krefft, 1955; Günther and Deckert, 1956; Koefoed, 1956; Günther and Deckert, 1959; Blache, 1960; Marshall, 1960; Cadenat, 1963; Krefft, 1963; Morrow, 1964c; Krefft, 1966; McAllister, 1967; Weitzman, 1967b; Gibbs, 1968; Quéro, 1969; Badcock, 1970; Geistdoerfer et al., 1971; Parin, 1971; Kotthaus, 1972; Parin et al., 1973; Goodyear, 1973; Nielsen, 1974; O'Day and Fernández, 1974; Clarke, 1974; Parin, 1974; Parin et al., 1974; Bekker et al., 1975; Badcock and Merret, 1976; Parin and Golovan, 1976; Krueger et al., 1977; Parin et al., 1977; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Goodyear, 1980; Gushchin and Kukuev, 1981; Kukuev, 1982; Murdy et al., 1983; Uyeno et al., 1983; Gibbs, 1984e; Fink, 1985; McKelvie and Haedrich, 1985; Goodyear and Gibbs, 1986; Campbell. and Herring, 1987; Bowmaker et al., 1988; Post, 1988; Goodyear, 1990; Mesinger and Case, 1990; Smale et al., 1995; Balanov and Fedorov, 1996; Magnússon, 1996; Sutton and Hopkins, 1996; Vinnichenko, 1997; Kukuev et al., 2000; Alpoim et al., 2002; Kukuev, 2002; Kukuev and Trunov, 2002; Sigurðsson et al., 2002; Moore et al., 2003a; Moore et al., 2003b; Fock et al., 2004

Global distribution: South Atlantic (to 40ºS or to 20ºS if *M. kreffti* of Goodyear [1980] is a distinct species). Indian Ocean (southwestern from 7ºN to 45ºS; south of India; eastern from 7ºN to 12ºS. Indo-Pacific. Pacific (from Japan to southeastern Australia and New Zealand; off Hawaii; equatorial to Gulf of Panama; South America and in the Bering Sea, 56ºN 169ºE).

Photostomias guernei Collett, 1889

Holotype: 38º 34' N 30º 43' W; MOM: 91 0050; “HIRONDELLE” 1887:111

Synonyms: *Thaumastomias atrox* Alcock, 1890; *Ultimostomias mirabilis* Beebe, 1933

References: Collett, 1889; Lütken, 1892; Goode and Bean, 1896; Collett, 1896; Dollo, 1904; Joubin, 1905; Zugmayer, 1911; Murray and Hjort, 1912; Jordan, 1923; Parr, 1927; Nusbaum-Hilarowicz, 1923; Parr, 1927; Norman, 1930; Regan and Trewavas, 1930; Borodin, 1931; Zugmayer, 1933; Parr, 1934; Nobre, 1935; Fowler, 1936; Beebe, 1937; Bertin, 1940; Belloc, 1949; Grey, 1955; Koefoed, 1956; Imai, 1957; Günther and Deckert, 1959; Blache, 1960; Marshall, 1960; Nicol, 1960; Cadenat, 1961; Lozano, 1963; Morrow, 1964c; Backus et al., 1965; Weitzman, 1967b; Backus et al., 1969; Karnella, 1969; Badcock, 1970; Geistdoerfer et al., 1971; Blaxter et al., 1971; Kort, 1971; Kotthaus, 1972; Goodyear, 1973; Parin et al., 1973; Clarke, 1974; Parin, 1974; Parin et al., 1974; Bekker et al., 1975; Badcock and Merret, 1976; Parin, 1976; Parin et al., 1976; Parin et al., 1977; Quéro, 1978 in Maurin et al.; Parin et al., 1978; Goodyear, 1980; Gushchin and Kukuev, 1981; Kukuev, 1982; Murdy et al., 1983; Gibbs, 1984e; Kawaguchi and Moser, 1984; Fink, 1985; Scott and Scott, 1988; Goodyear, 1990; Mesinger and Case, 1990; Brooks and Saenger, 1991; Sutton and Hopkins, 1996; Vinnichenko, 1997; Alpoim et al., 2002; Kukuev, 2002; Moore et al., 2003a; Moore et al., 2003b; Wienerroither, 2003

Global distribution: South Atlantic (to 20ºS, 30ºW). Indian (from 10ºN to 20ºS). Indo-Pacific. Pacific (from 30ºN to 30ºS).

Observations: Goodyear (1980) described four additional species of *Photostomias*. The systematics of the genus is being revised (see Chapter 5).

Pachystomias microdon (Günther, 1878)

Holotype: from off NW coast of Australia; BMNH

Synonyms: *Echiostoma microdon* Günther, 1878; / *P. atlanticus* Regan and Trewavas, 1930; Beebe, 1937; Beebe and Crane, 1939 / *Aristostomias brattströmii* Koefoed, 1956

References: Günther, 1878; Günther, 1887; Lendenfeld, 1887; Goode and Bean, 1896; Parr, 1927; Regan and Trewavas, 1930; Roule and Angel, 1933; Beebe, 1937; Beebe and Crane, 1939; Koefoed, 1956; Morrow and Gibbs, 1964; Kotthaus, 1968; Denton, 1971; Rass, 1971; Hulley, 1972; Clarke, 1974, Parin et al., 1974; Parin et al., 1976; Gushchin and Kukuev, 1981; Kukuev, 1982; Gibbs, 1984d; Fink, 1985; Gibbs, 1986d; Bowmaker et al., 1988; Gibbs and Barnett, 1990; Balanov and Fedorov, 1996; Sigurðsson et al., 2002; Moore et al., 2003a

Global distribution: South Atlantic (eastern to 40ºS). Indian (western from 0º to 10ºS). Indo-Pacific. Pacific (northeastern Australia; off Japan; off Hawaii; eastern from 0º to 20ºS; 53ºN 179ºW).

Observations: Fink (1985) and Goodyear (1980) gave evidences that *P. microdon* is a member of the malacosteids.

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Appendix F
Atlas of North Atlantic Stomiidae species

This atlas illustrates the distribution of stomiid species in the North Atlantic. Dots in the maps represent collections sites (net-hauls or *field_code*). One dot may represent more than one net-haul. For instance, in stations performed with multi-closing sampling devices those dots may represent tens of net-hauls and specimens. Grey dots indicate net-hauls that were used to compute the sampling effort (Chapter 4); black dots represent occurrences without gear information, collections from bottom trawls or from non-standard gears (Chapter 3). One dot can represent more than one net-haul. The total stations considered are plotted in Figure 2.3. Kriging interpolated the spatial distribution of species relative abundance (*n_spec/std_h*) per unit area (s*q_5x5*; see Fig. 2.2b). Only the lower contour produced by that analysis is shown. The eco-biogeographic provinces (*Lgh_P*; Longhurst, 1998b; Fig. 2.2a) were superimposed to the distribution maps. The global distribution of the North Atlantic stomiid species (outside the North Atlantic) is summarised in Appendix E. The number of individuals (n), the distribution pattern and sub-pattern (see Chapter 6) are given for each species mapped.

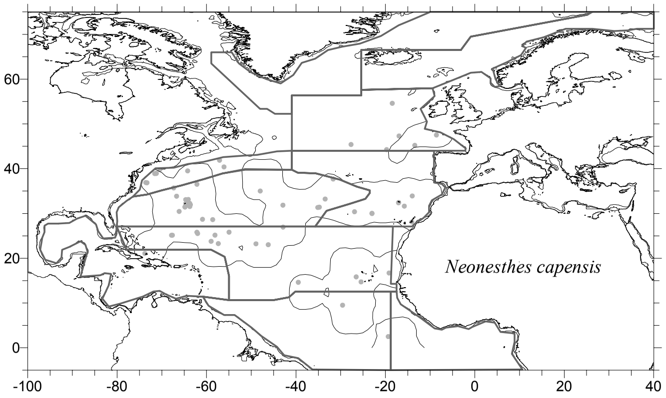


Fig. F1. *Neonesthes capensis* (107): Subtropical complex; Subtropical - Tropical gyre / Eastern tropical.

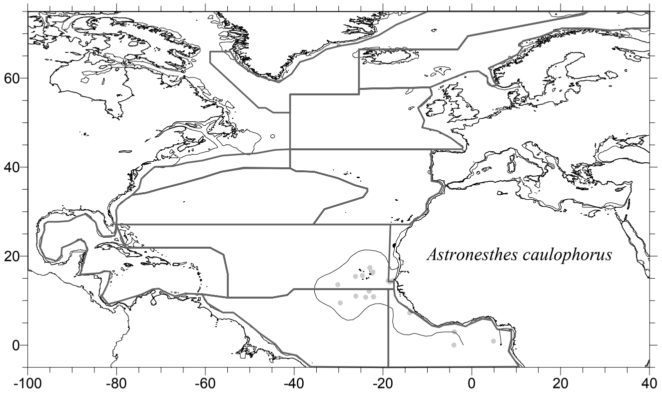


Fig. F2. *Astronesthes caulophorus* (36): Eastern Tropical - Equatorial (east); large range (distant neritic).

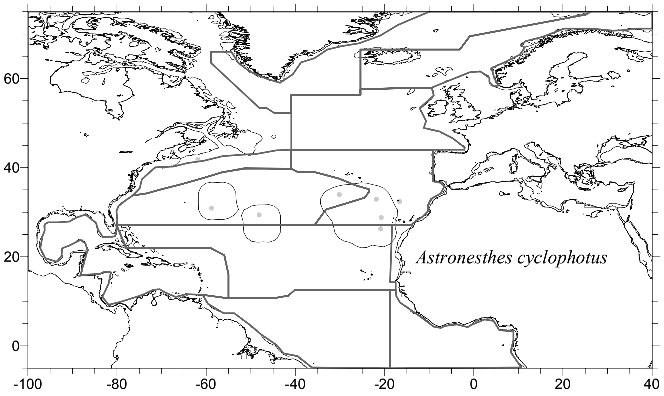


Fig. F3. *Astronesthes cyclophotus* (10): Subtropical (east); North Atlantic endemic.

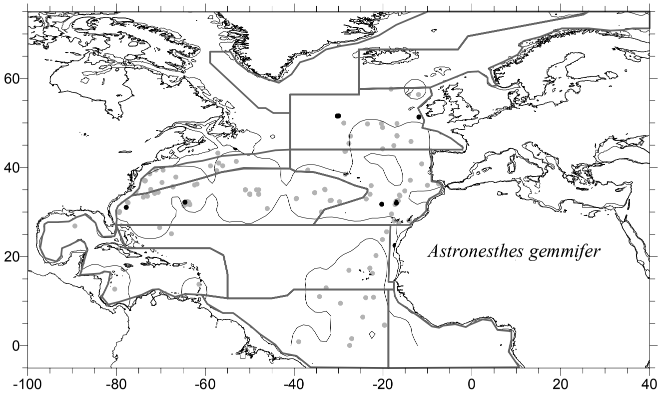


Fig. F4. *Astronesthes gemmifer* (208): Subtropical complex; Subtropical - Eastern tropical - Equatorial (east).

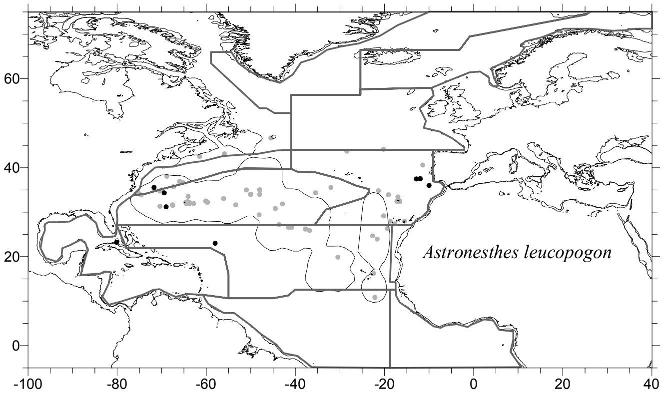


Fig. F5. *Astronesthes leucopogon* (154): Subtropical complex; Subtropical - Eastern tropical.

Neonethes / Astronesthes

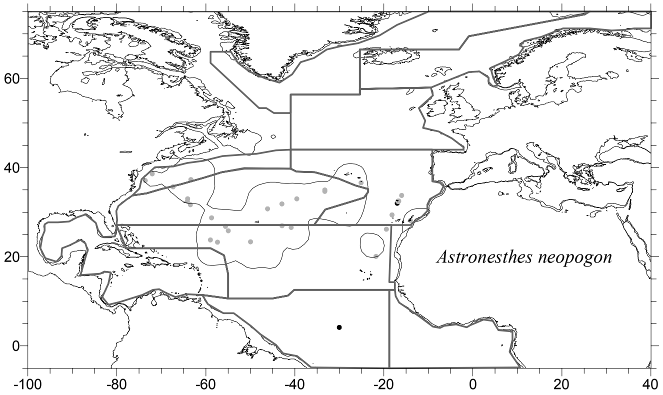


Fig. F6. *Astronesthes neopogon* (34): Western Tropical Gyre complex; Tropical gyre - Subtropical; North Atlantic endemic.

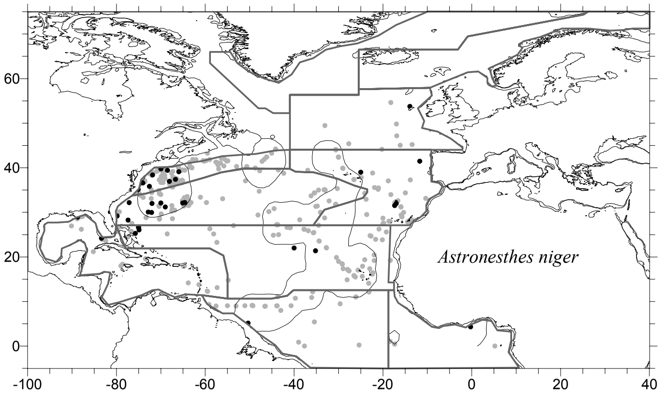


Fig. F7. *Astronesthes niger* (1760): Uncertain pattern.

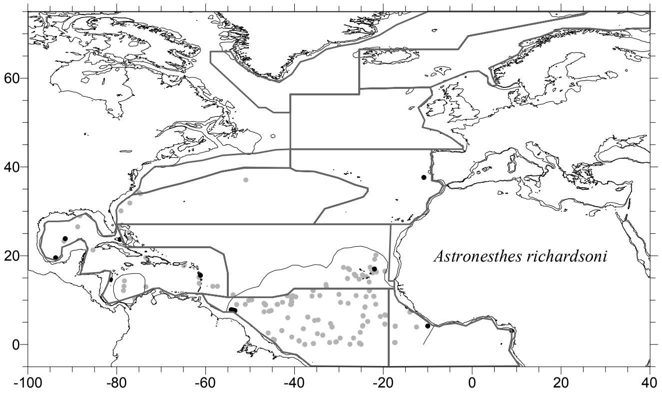


Fig. F8. *Astronesthes richardsoni* (692): Equatorial; Eastern Tropical – Caribbean.

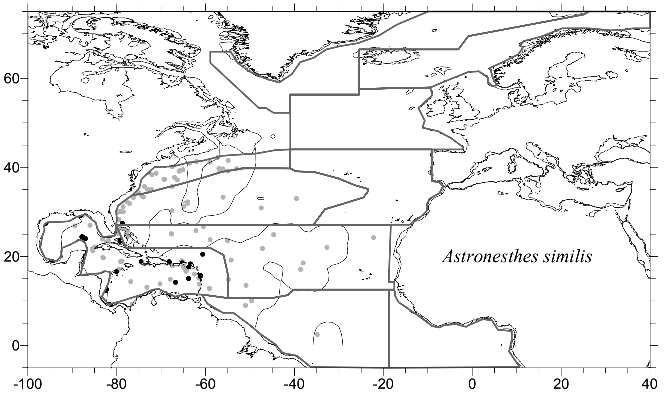


Fig. F9. *Astronesthes similis* (200): Caribbean complex; Caribbean - Western Tropical.

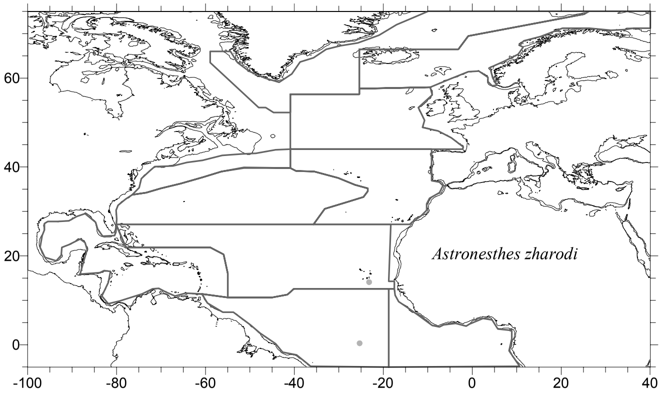


Fig. F10. *Astronesthes zharodi* (2): Eastern Tropical - Equatorial; North Atlantic endemic.

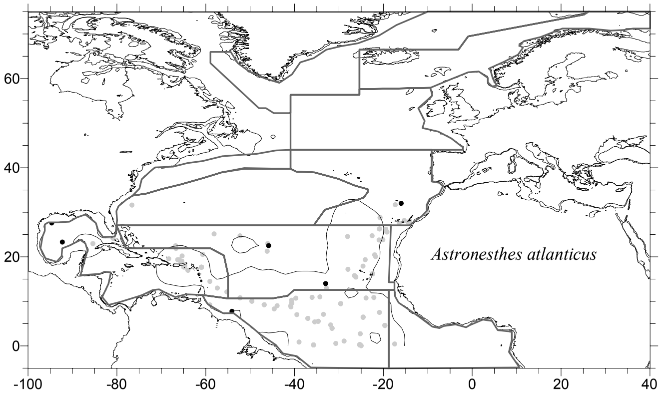


Fig. F11. *Astronesthes atlanticus* (239): Equatorial (west) - Eastern Tropical – Caribbean.

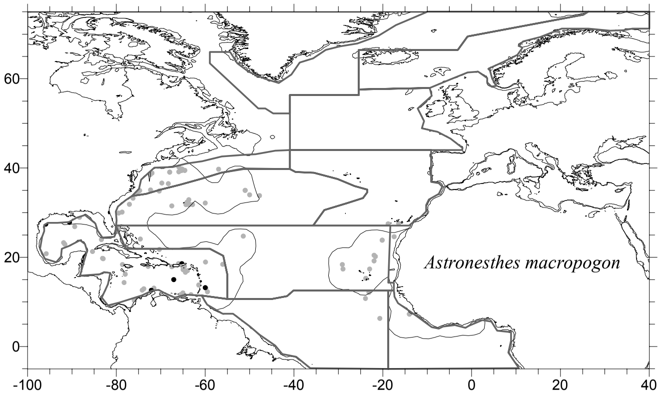


Fig. F12. *Astronesthes macropogon* (166): Amphi-Atlantic (distant neritic); Tropical - Equatorial (east).

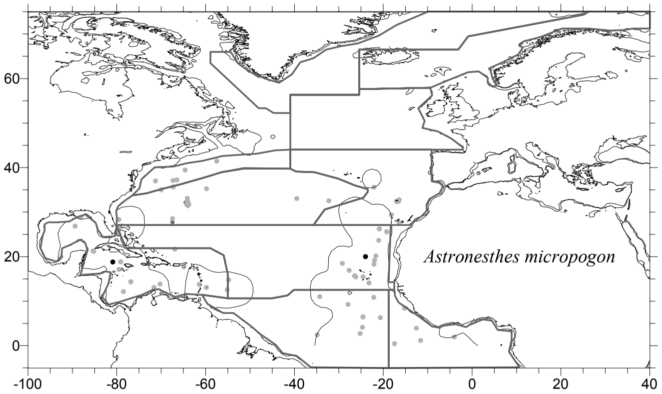


Fig. F13. *Astronesthes micropogon* (117): Amphi-Atlantic (distant neritic); Tropical - Equatorial (east).

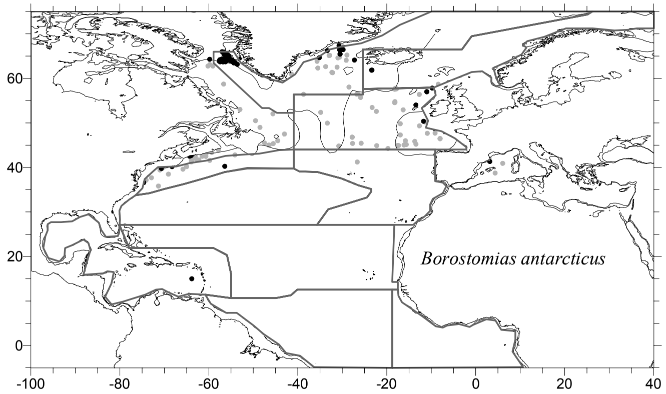


Fig. F14. *Borostomias antarcticus* (183): Polar - Boreal / Mediterranean (west).

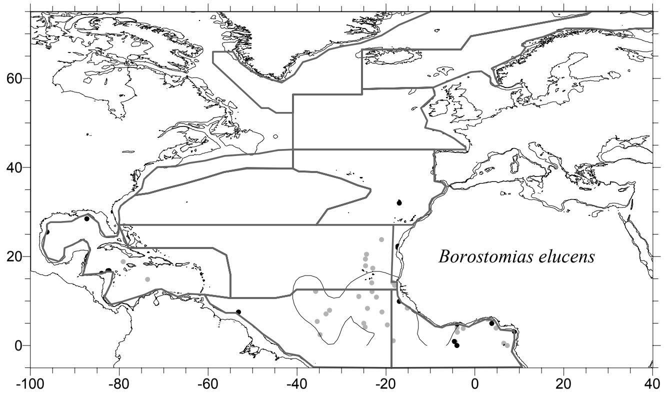


Fig. F15. *Borostomias elucens* (121): Eastern Tropical – Equatorial (east) (distant neritic).

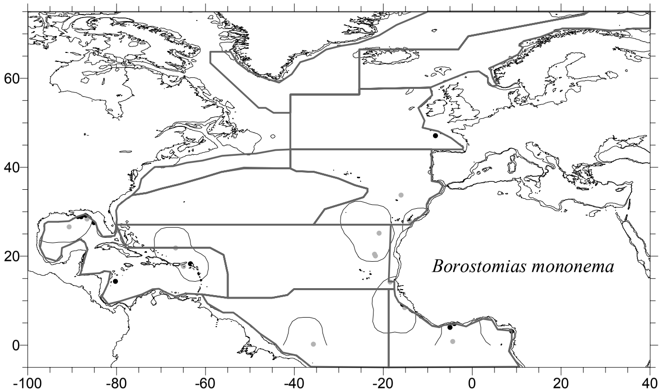


Fig. F16. *Borostomias mononema* (24): Amphi-Atlantic (distant neritic); Tropical - Equatorial (east).

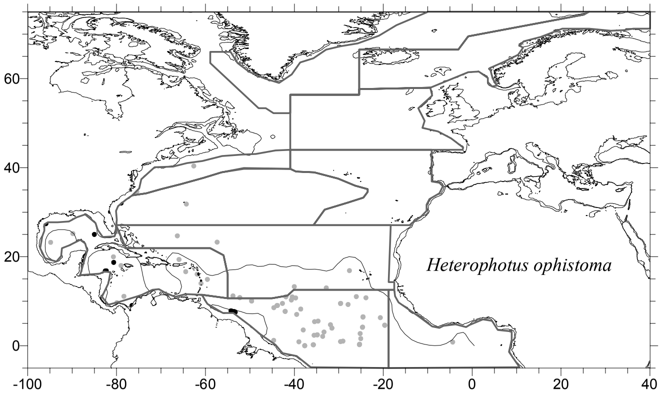


Fig. F17. *Heterophotus ophistoma* (137): Equatorial (west) – Caribbean.

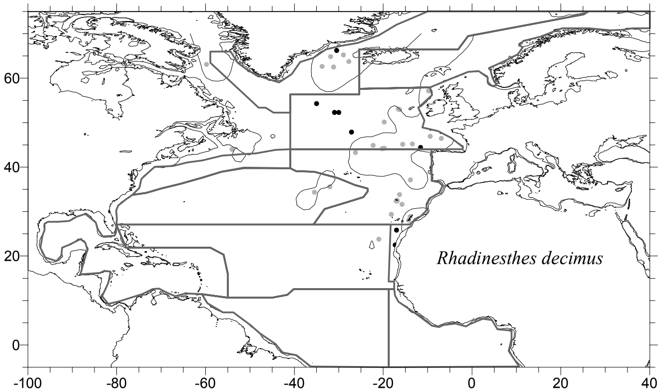


Fig. F18. *Rhadinesthes decimus* (38): Extended Eastern; Polar - Eastern Tropical.

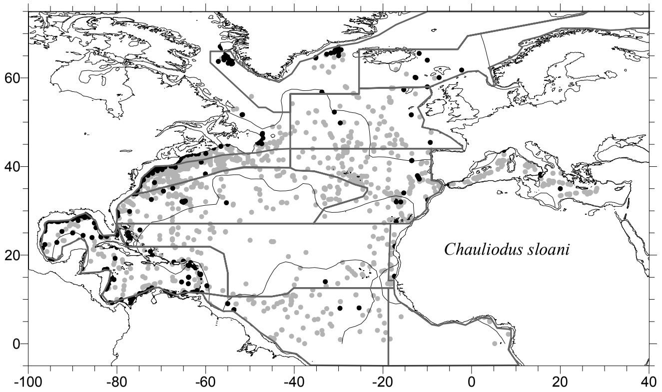


Fig. F19. *Chauliodus sloani* (11636): Widespread (anti-central).

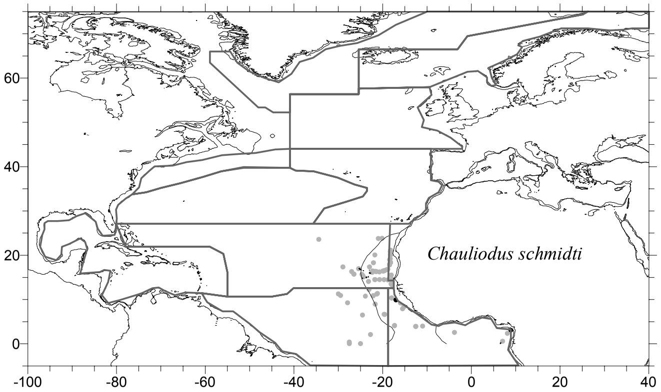


Fig. F20. *Chauliodus schmidti* (452): Eastern Tropical - Equatorial (east); large range (distant neritic).

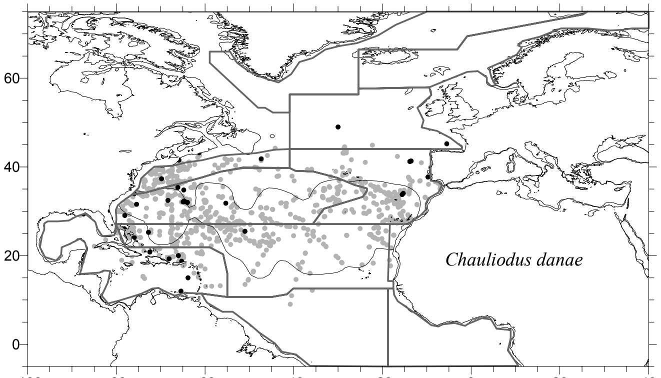


Fig. F21. *Chauliodus danae* (7078): Tropical - Subtropical; North Atlantic endemic.

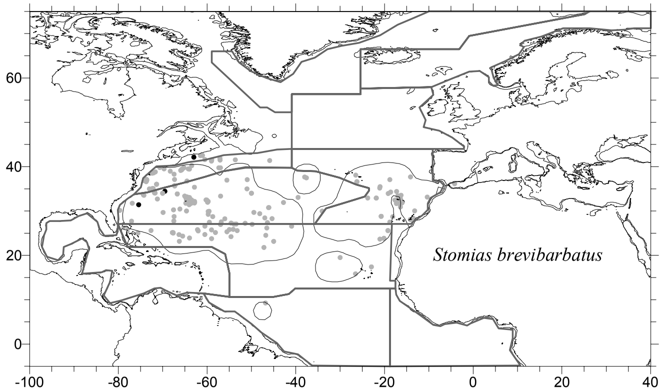


Fig. F22. *Stomias brevibarbatus* (488): Subtropical complex; Subtropical - Tropical gyre - Eastern tropical; North Atlantic endemic.

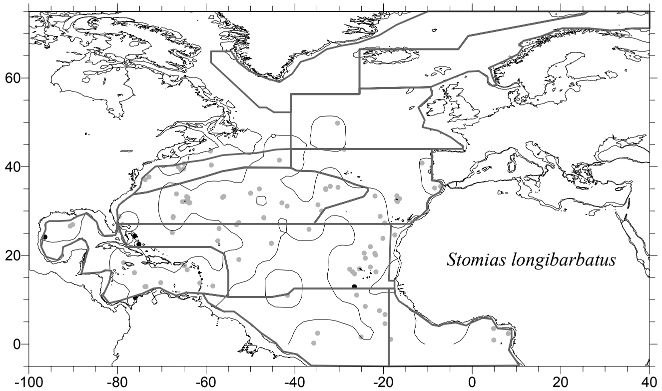


Fig. F23. *Stomias longibarbatus* (119): Broadly Tropical.

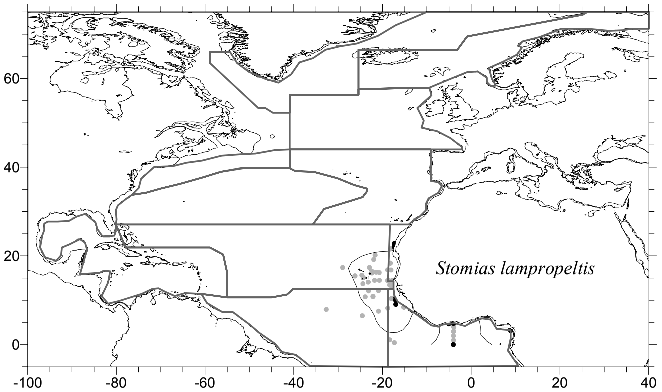


Fig. F24. *Stomias lampropeltis* (280): Eastern Tropical - Equatorial (east); large range (distant neritic).

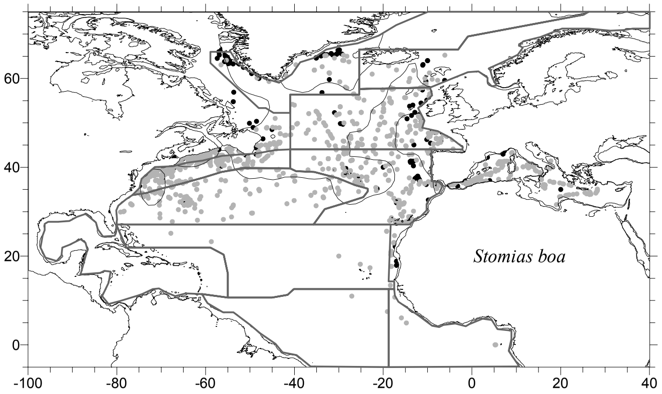


Fig. F25. *Stomias boa* (10233): Boreal - Subtropical (east) (*S. b. ferox*); Mediterranean - Eastern Tropical (*S. b. boa*).

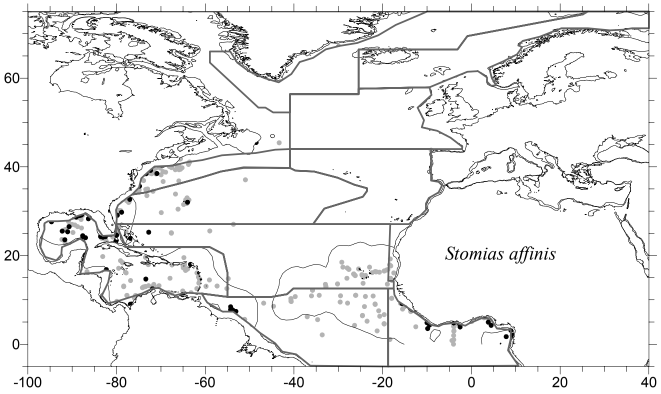


Fig. F26. *Stomias affinis* (783): Amphi-Atlantic (distant neritic); Tropical - Equatorial (east).

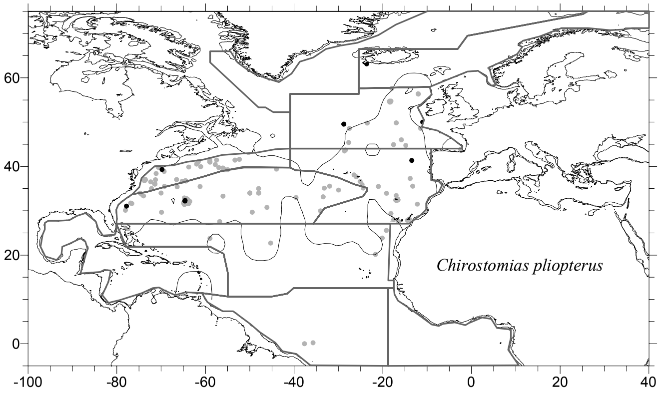


Fig. F27. *Chirostomias pliopterus* (203): Subtropical complex; Subtropical - Boreal; North Atlantic endemic.

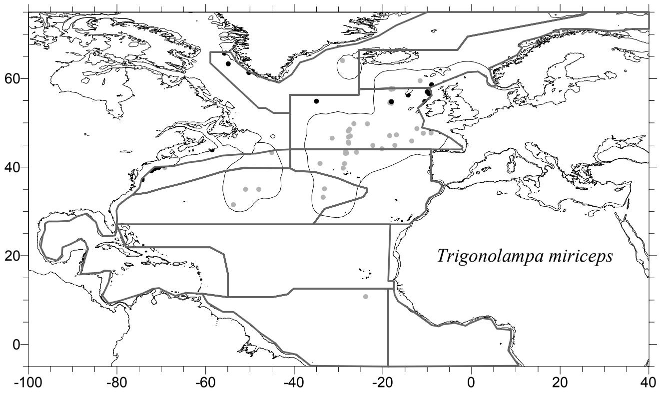


Fig. F28. *Trigonolampa miriceps* (72): Boreal (east).

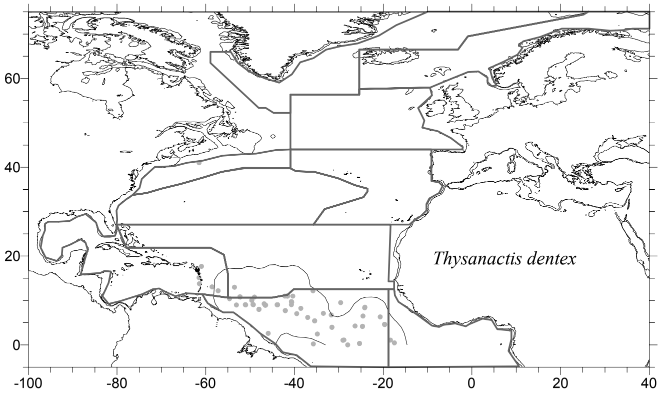


Fig. F29. *Thysanactis dentex* (146): Equatorial (west).

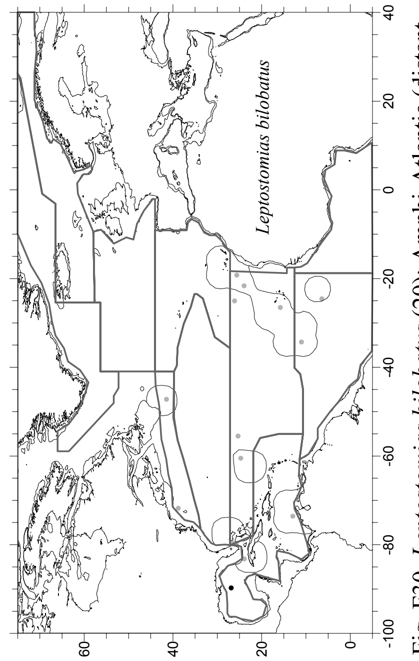


Fig. F30. *Leptostomias bilobatus* (20): Amphi-Atlantic (distant neritic); Tropical.

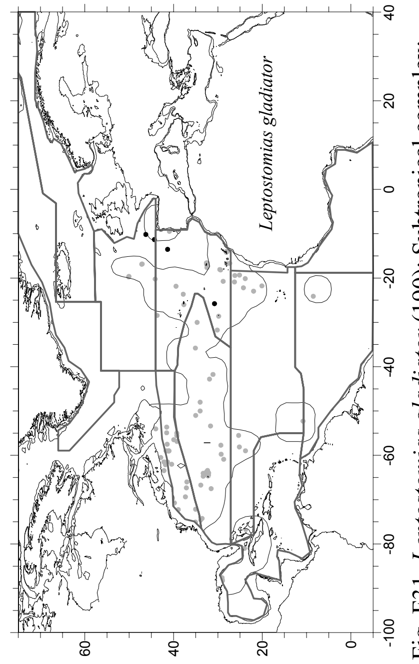


Fig. F31. *Leptostomias gladiator* (190): Subtropical complex; Subtropical - Eastern tropical.

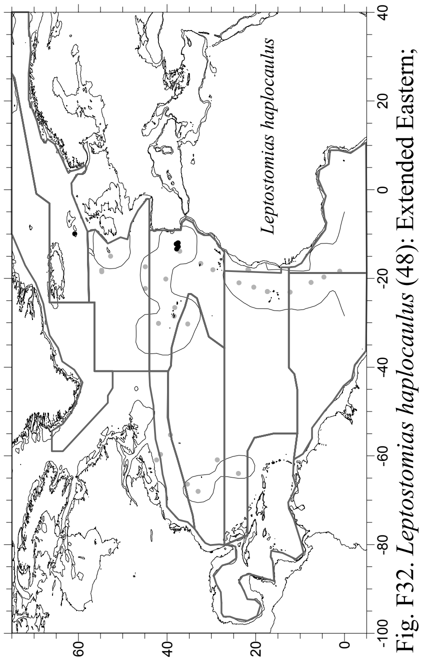


Fig. F32. *Leptostomias haplocaulus* (48): Extended Eastern; Equatorial - Tropical – Subtropical.

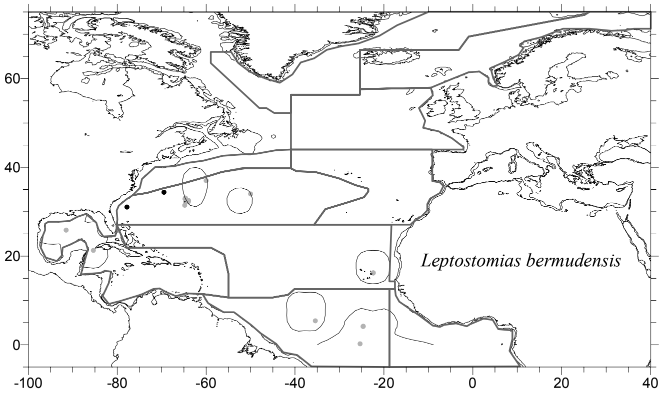


Fig. F33. *Leptostomias bermudensis* (23): Uncertain pattern.

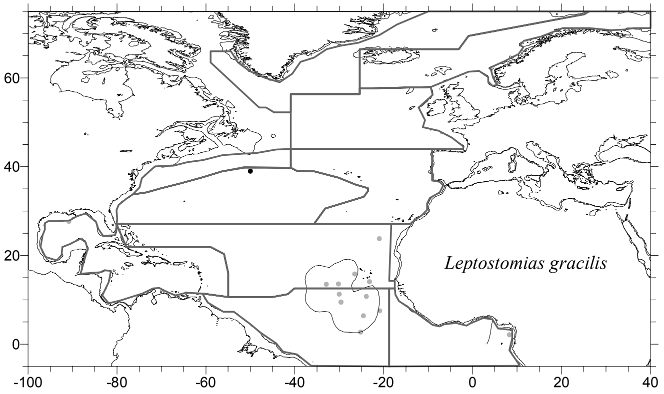


Fig. F34. *Leptostomias gracilis* (18): Eastern Tropical – Equatorial (east); limited range (distant neritic).

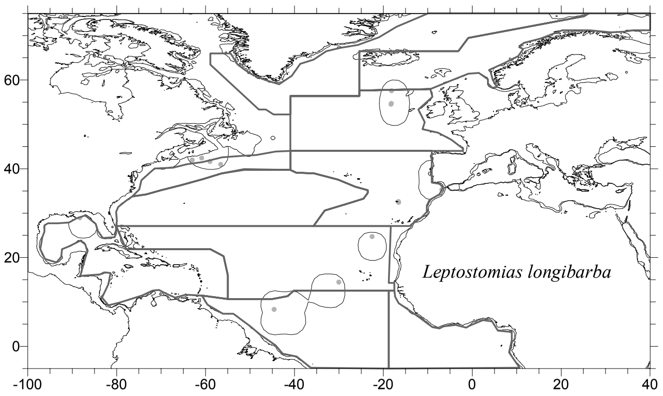


Fig. F35. *Leptostomias longibarba* (23): Uncertain pattern.

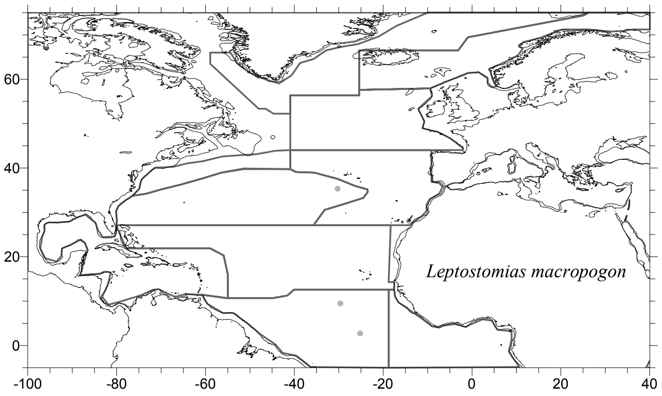


Fig. F36. *Leptostomias macropogon* (7): Uncertain pattern; North Atlantic endemic.

Leptostomias

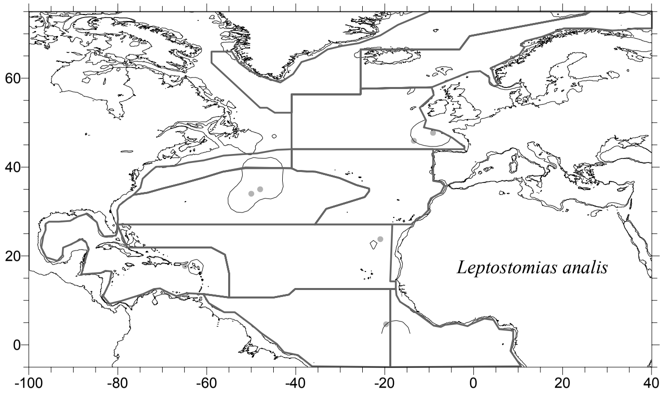


Fig. F37. *Leptostomias analis* (7): Uncertain pattern.

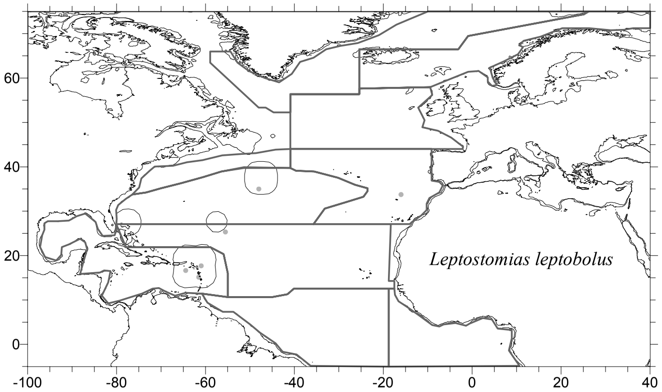


Fig. F38. *Leptostomias leptobolus* (7): Uncertain pattern.

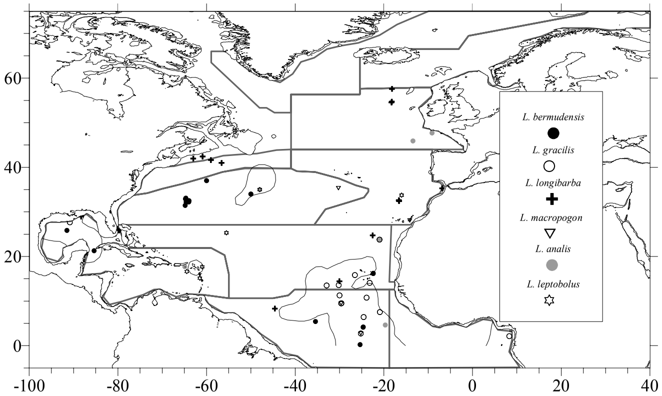


Fig. F39. Distribution of *Leptostomias* spp. that may be prove to be synonyms .(see comments on Chapter 5)

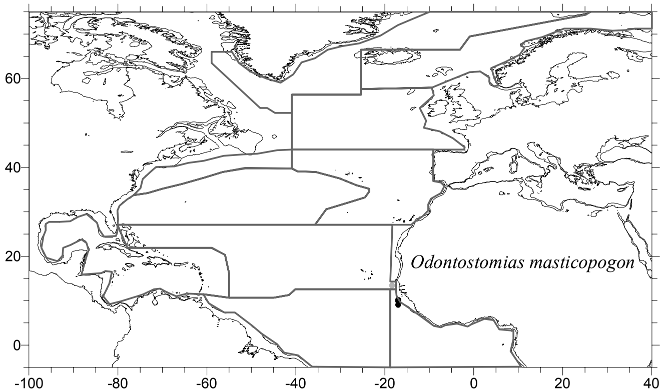


Fig. F40. *Odontostomias masticopogon* (1): Eastern Tropical - Equatorial; Eastern Tropical; limited range (distant neritic).

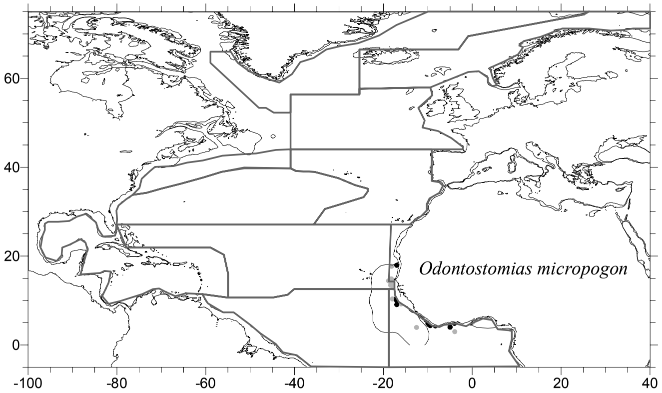


Fig. F41. *Odontostomias micropogon* (86): Eastern Tropical - Equatorial (east); large range (distant neritic).

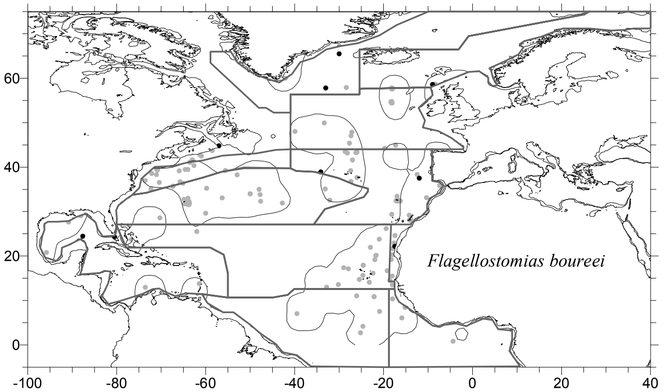


Fig. F42. *Flagellostomias boureei* (192): Subtropical complex; Subtropical - Boreal (east) / Eastern Tropical – Equatorial.

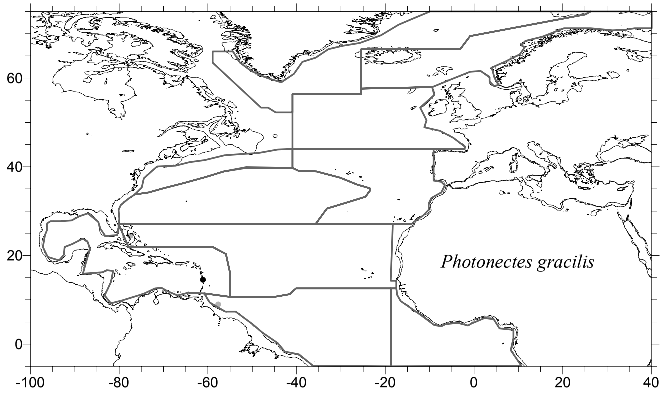


Fig. F43. *Photonectes gracilis* (2): Equatorial (west) - Caribbean (distant neritic).

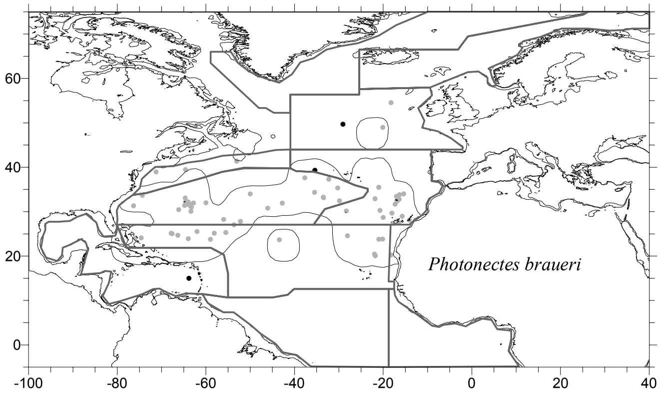


Fig. F44. *Photonectes braueri* (91): Western Tropical Gyre complex; Tropical gyre - Subtropical - Eastern tropical.

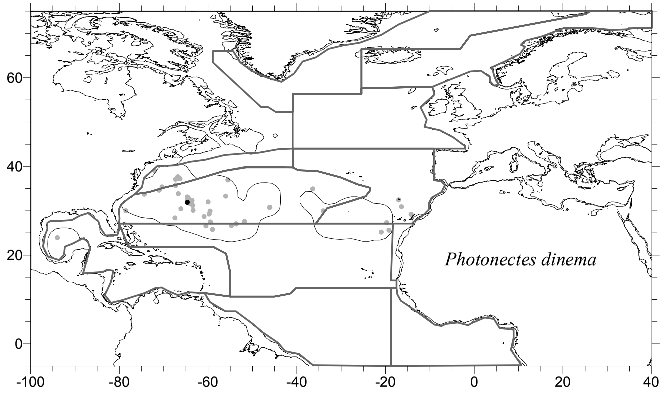


Fig. F45. *Photonectes dinema* (94): Subtropical (west); North Atlantic endemic.

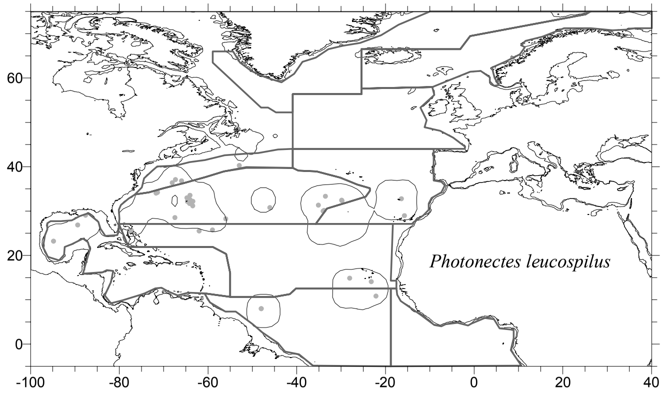


Fig. F46. *Photonectes leucospilus* (67): Subtropical complex; Subtropical (west) / Eastern tropical.

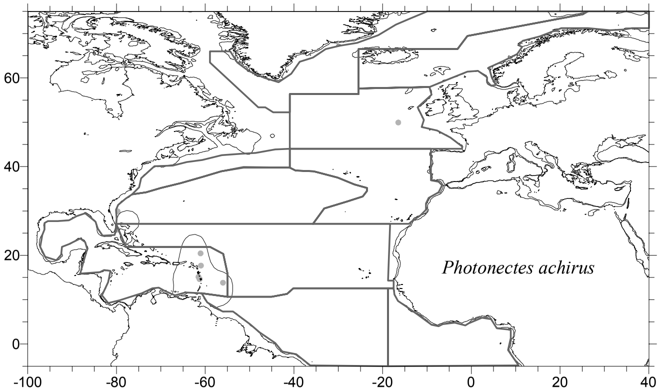


Fig. F47. *Photonectes achirus* (9): Caribbean (distant neritic).

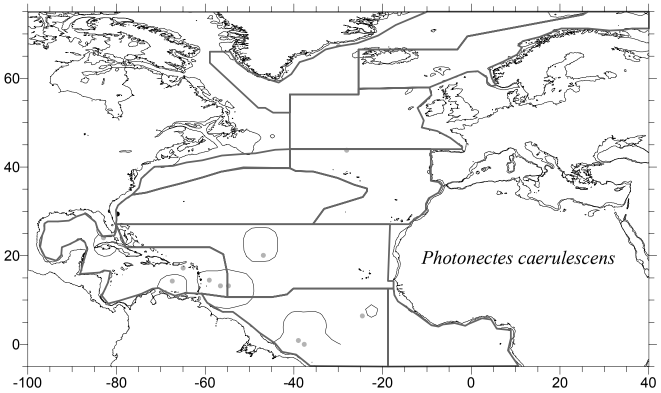


Fig. F48. *Photonectes caerulescens* (16): Equatorial (west) - Caribbean (distant neritic).

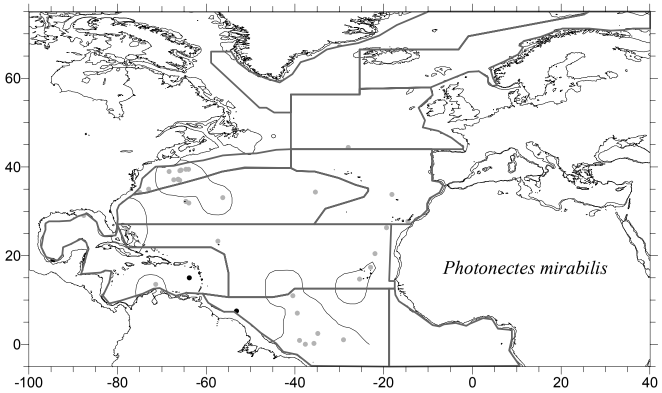


Fig. F49. *Photonectes mirabilis* (58): Equatorial (west) - Eastern Tropical – Caribbean.

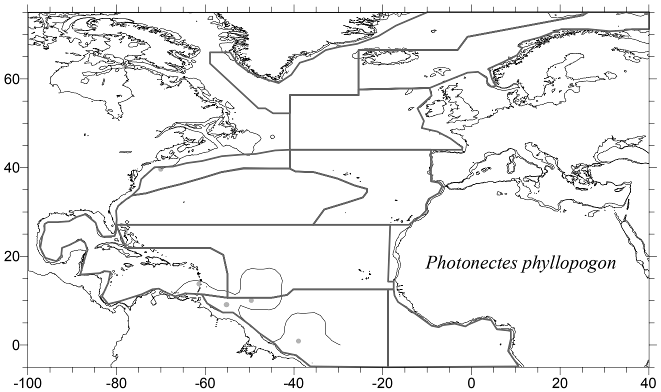


Fig. F50. *Photonectes phyllopogon* (12): Equatorial (west) - Caribbean (distant neritic).

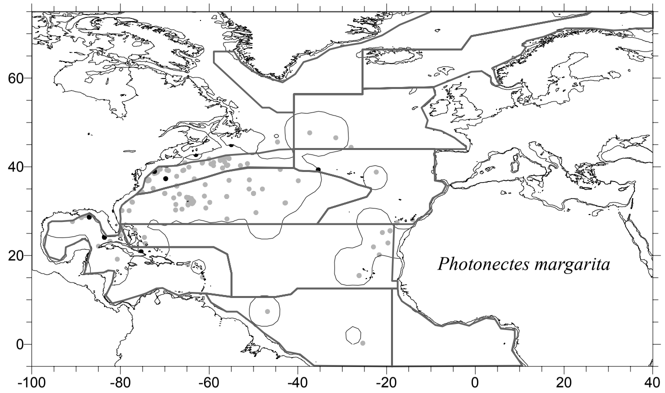


Fig. F51. *Photonectes margarita* (218): Subtropical complex; Subtropical (west) / Eastern tropical.

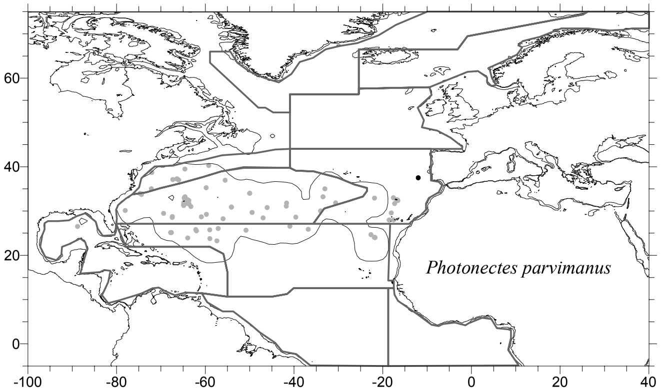


Fig. F52. *Photonectes parvimanus* (99): Subtropical (west) - Tropical Gyre.

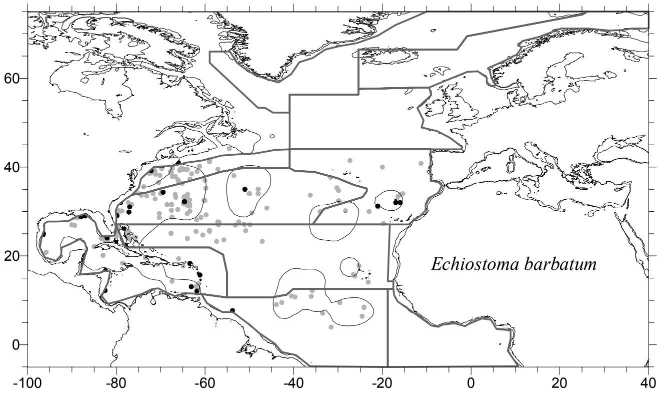


Fig. F53. *Echiostoma barbatum* (551): Caribbean complex; Caribbean - Tropical Gyre - Subtropical (west) / Equatorial (west).

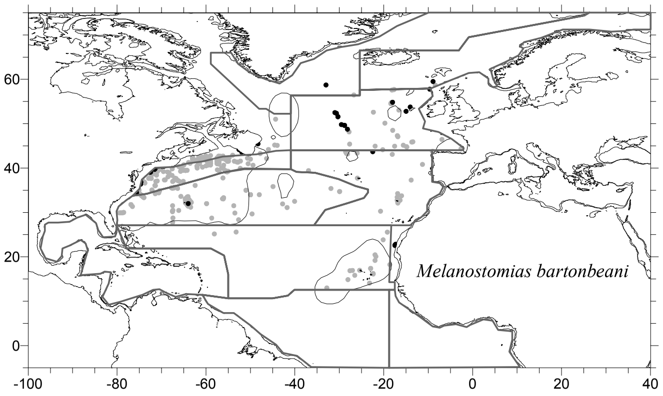


Fig. F54. *Melanostomias bartonbeani* (1142): Subtropical complex; Subtropical - Boreal - Eastern Tropical.

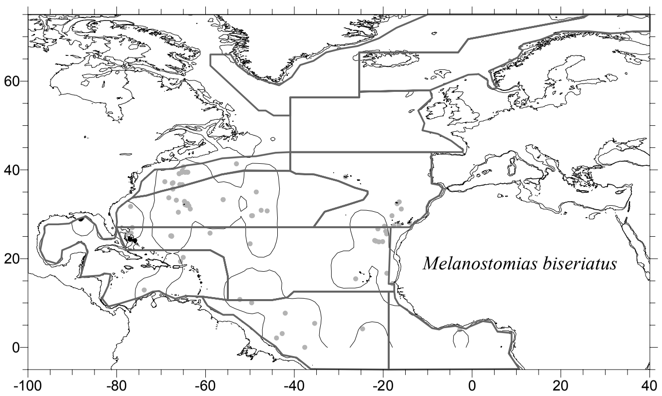


Fig. F55. *Melanostomias biseriatus* (117): Subtropical complex; Subtropical (west) - Caribbean / Equatorial (west) / Eastern tropical.

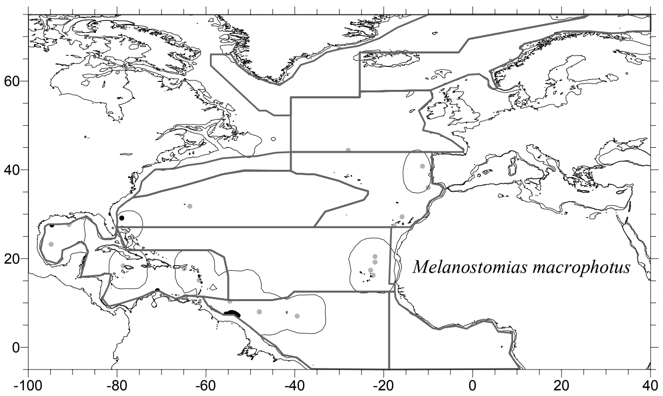


Fig. F56. *Melanostomias macrophotus* (36): Amphi-Atlantic (distant neritic); Tropical - Equatorial (west).

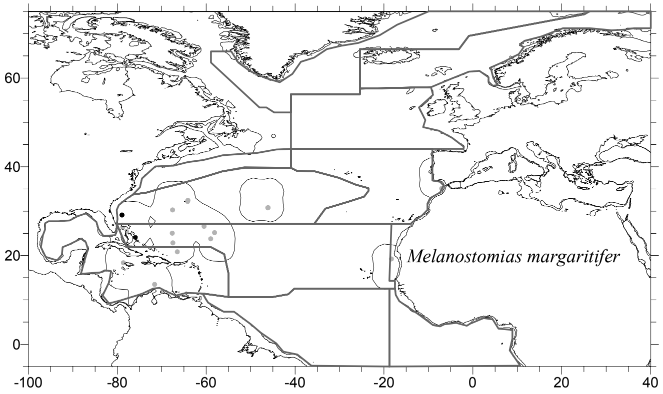


Fig. F57. *Melanostomias margaritifer* (19): Western Tropical Gyre complex; Tropical Gyre – Caribbean.

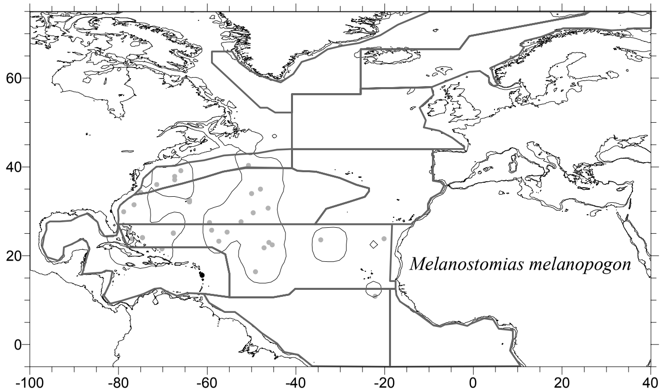


Fig. F58. *Melanostomias melanopogon* (55): Western Tropical Gyre complex; Tropical gyre - Subtropical (west); North Atlantic endemic.

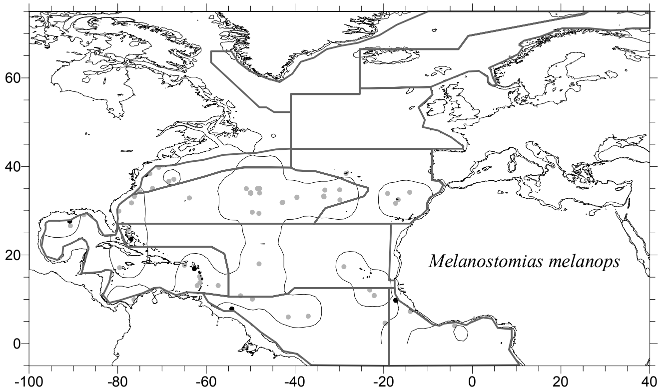


Fig. F59. *Melanostomias melanops* (94): Equatorial complex; Equatorial (west) - Caribbean / Subtropical (west) / Eastern tropical - Equatorial (east).

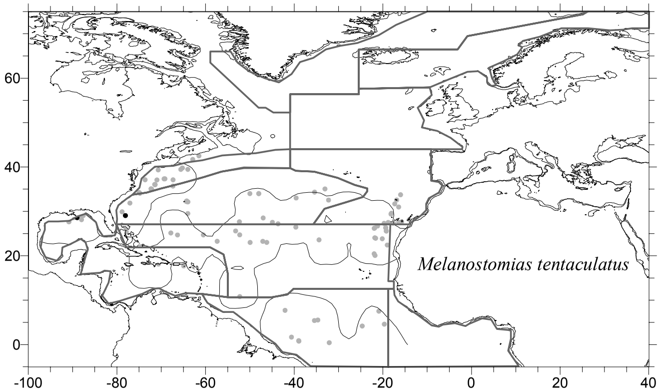


Fig. F60. *Melanostomias tentaculatus* (166): Tropical - Equatorial; Northern Tropical - Caribbean / Equatorial (west).

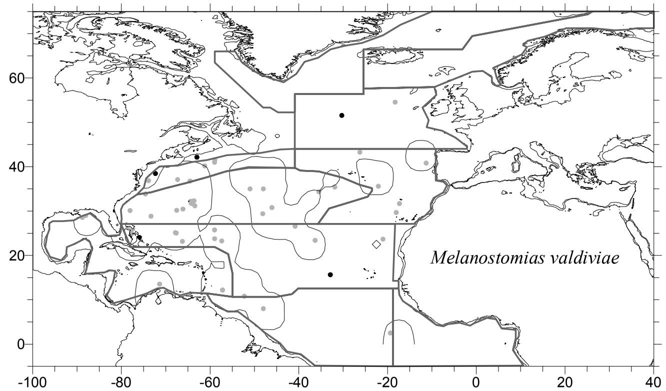


Fig. F61. *Melanostomias valdiviae* (80): Western Tropical Gyre complex; Tropical Gyre - Caribbean - Subtropical (west).

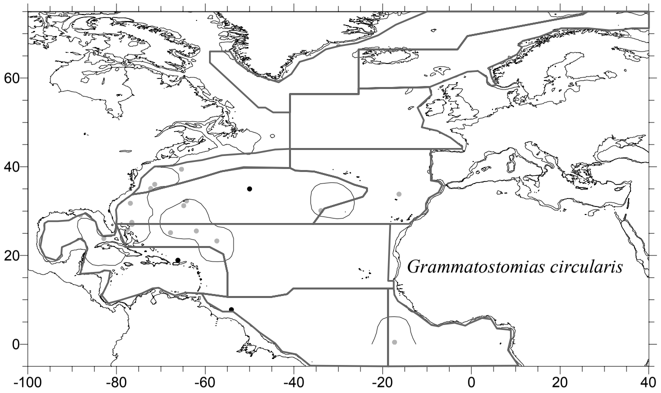


Fig. F62. *Grammatostomias circularis* (20): Caribbean complex; Caribbean - Tropical Gyre - Subtropical (west).

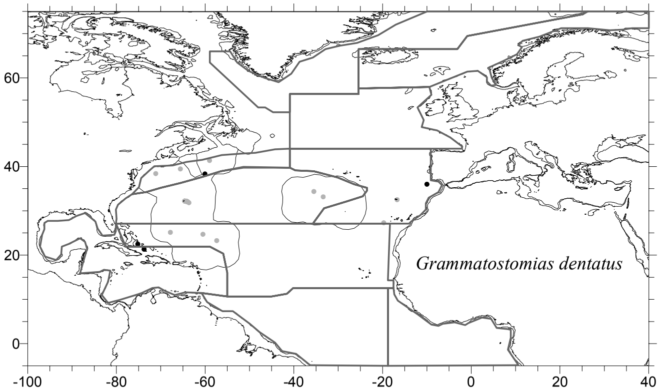


Fig. F63. *Grammatostomias dentatus* (20): Subtropical (west) - Tropical Gyre.

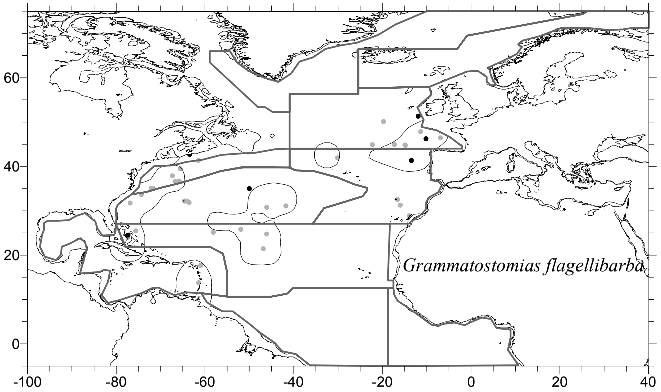


Fig. F64. *Grammatostomias flagellibarba* (36): Western Tropical Gyre complex; Tropical Gyre - Subtropical / Boreal (east); North Atlantic endemic.

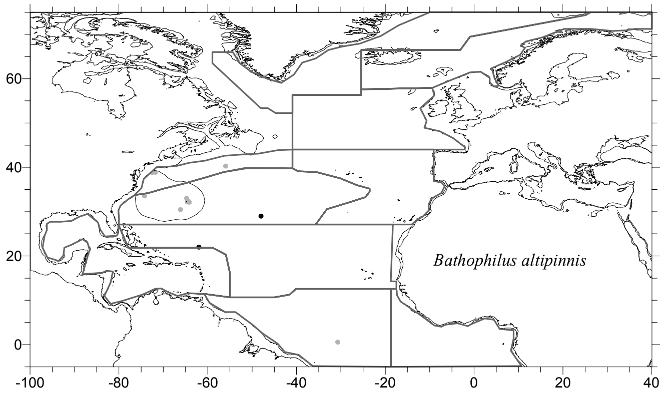


Fig. F65. *Bathophilus altipinnis* (10): Subtropical (west).

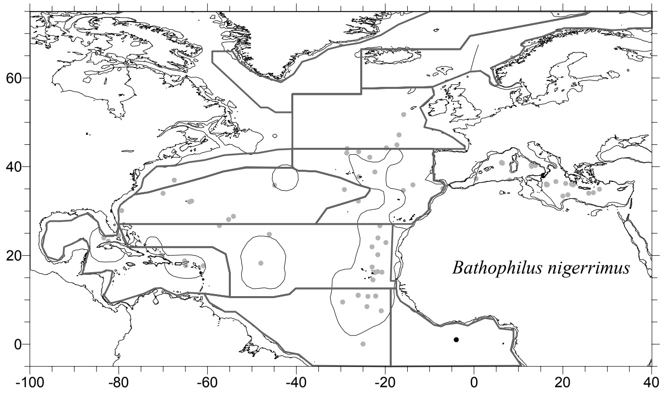


Fig. F66. *Bathophilus nigerrimus* (100): Mediterranean - Extended Eastern.

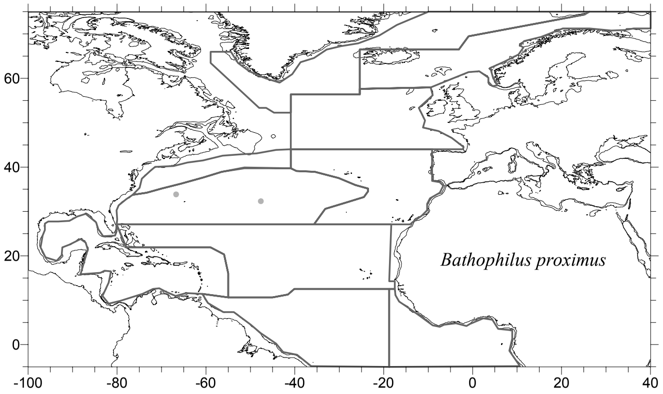


Fig. F67. *Bathophilus proximus* (3): Subtropical (west); North Atlantic endemic.

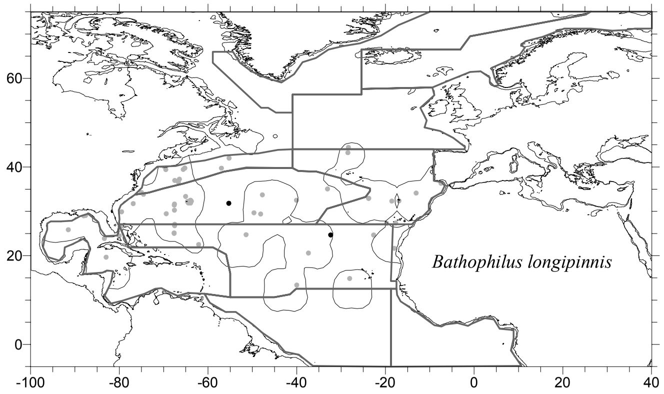


Fig. F68. *Bathophilus longipinnis* (67): Tropical – Subtropical.

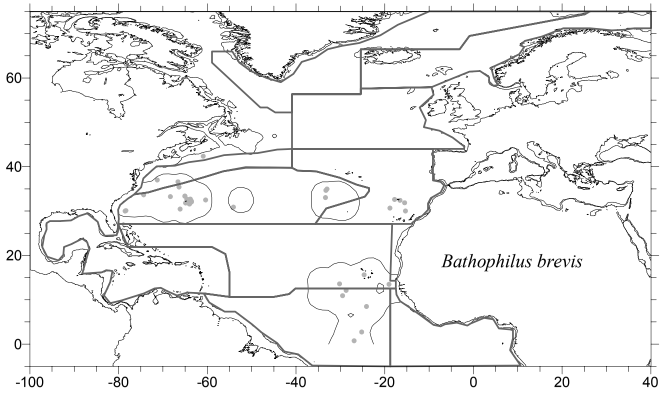


Fig. F69. *Bathophilus brevis* (57): Subtropical complex;
Subtropical (west) / Eastern tropical - Equatorial (east).

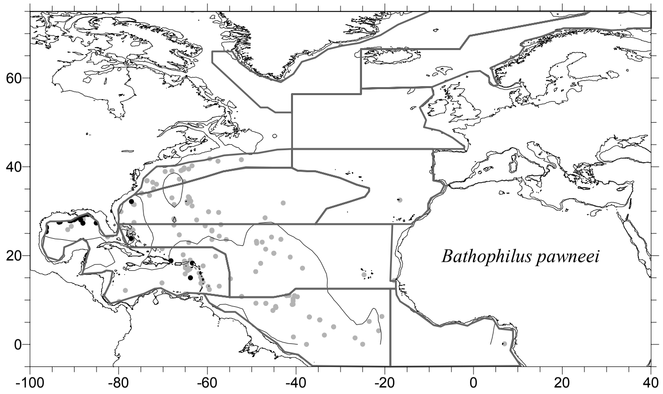


Fig. F70. *Bathophilus pawneei* (312): Caribbean complex;
Caribbean - Tropical (west) - Equatorial (west).

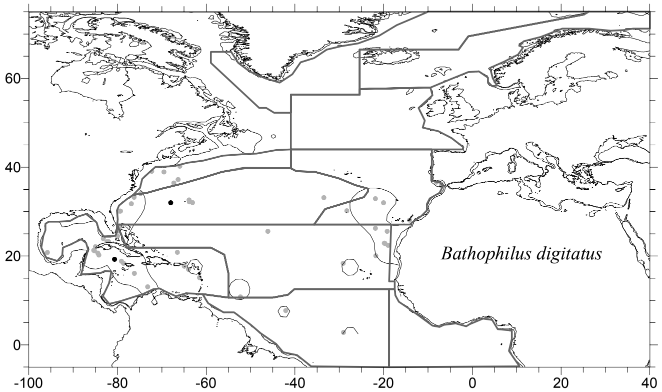


Fig. F71. *Bathophilus digitatus* (62): Amphi-Atlantic (distant neritic); Tropical.

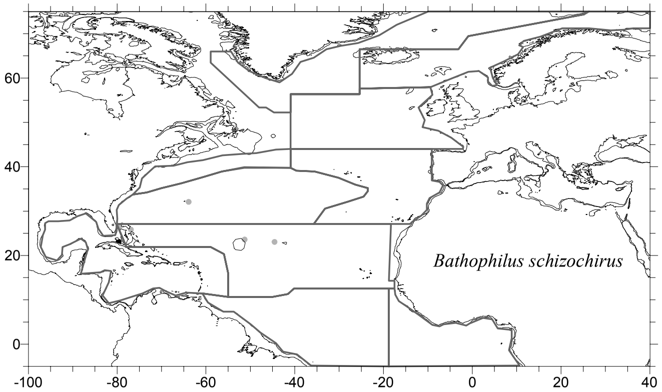


Fig. F72. *Bathophilus schizochirus* (5): Western Tropical Gyre.

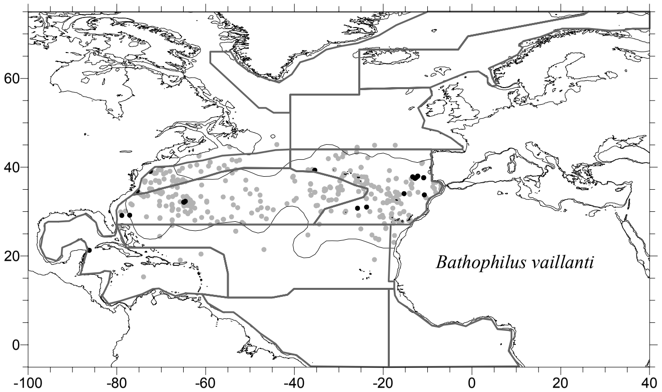


Fig. F73. *Bathophilus vaillanti* (852): Subtropical; North Atlantic endemic.

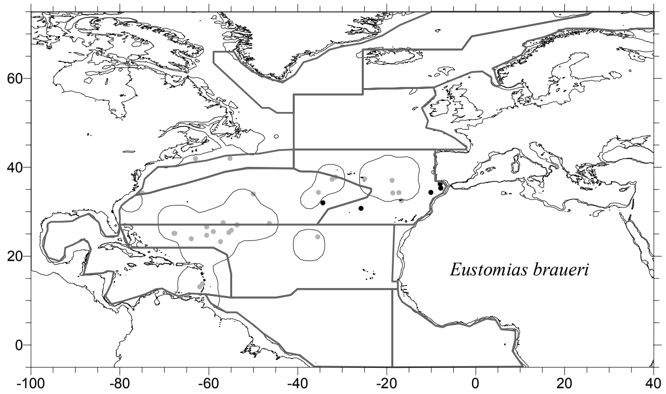


Fig. F74. *Eustomias braueri* (34): Western Tropical Gyre complex; Tropical gyre / Subtropical (east).

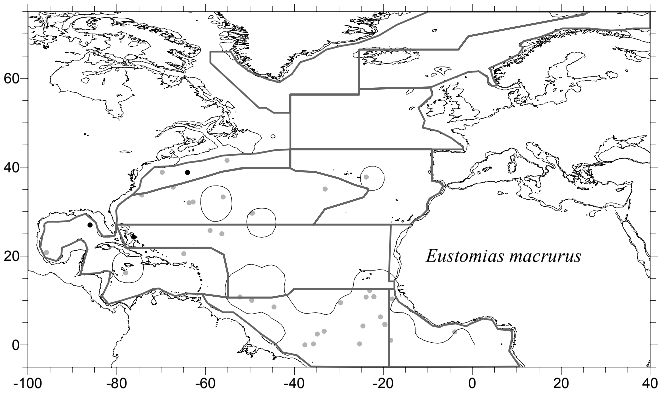


Fig. F75. *Eustomias macrurus* (55): Equatorial.

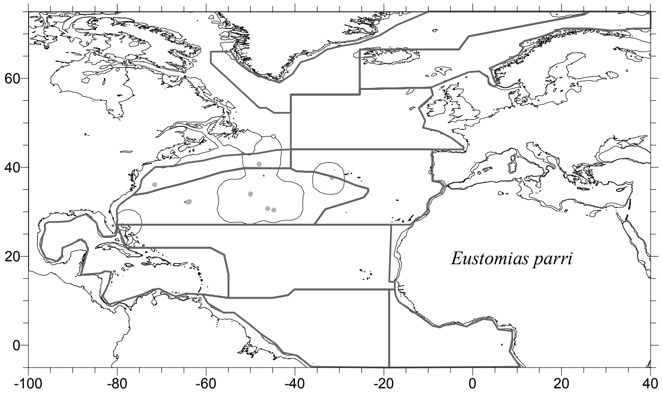


Fig. F76. *Eustomias parri* (10): Subtropical (west); North Atlantic endemic.

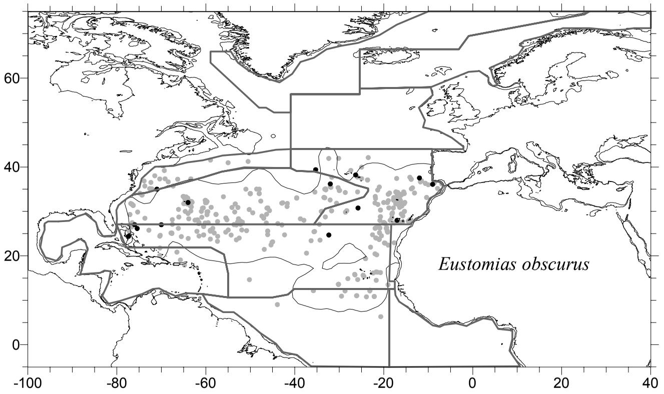


Fig. F77. *Eustomias obscurus* (943): Subtropical complex; Subtropical - Northern Tropical - Eastern tropical.

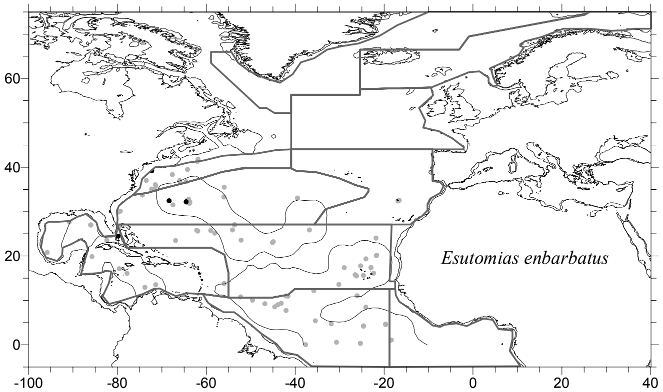


Fig. F78. *Eustomias enbarbatus* (154): Equatorial complex; Equatorial (west) - Eastern Tropical – Western Tropical.

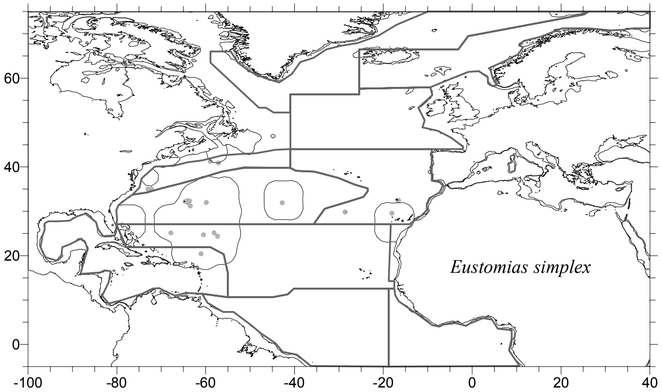


Fig. F79. *Eustomias simplex* (41): Western Tropical Gyre complex; Tropical Gyre - Subtropical (west).

Eustomias (Spilostomias; Rhynchostomias; Haploclonus)

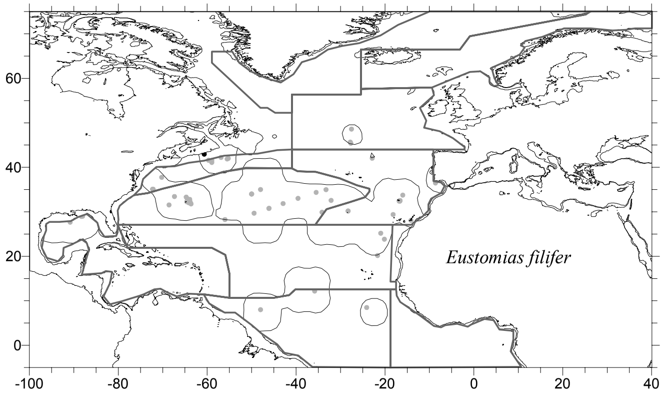


Fig. F80. *Eustomias filifer* (92): Subtropical complex; Subtropical - Eastern tropical.

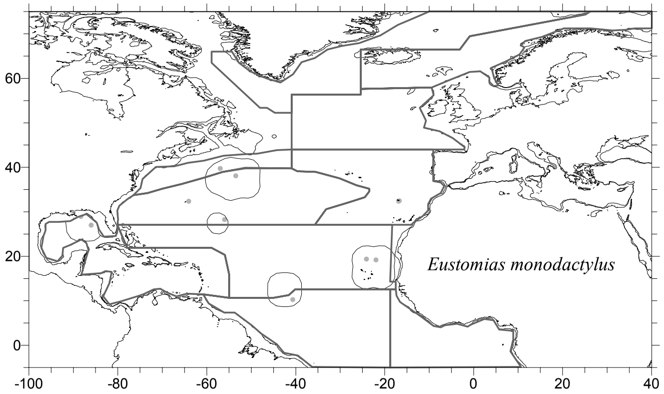


Fig. F81. *Eustomias monodactylus* (13): Eastern Tropical complex; Eastern tropical / Caribbean - Subtropical; North Atlantic endemic.

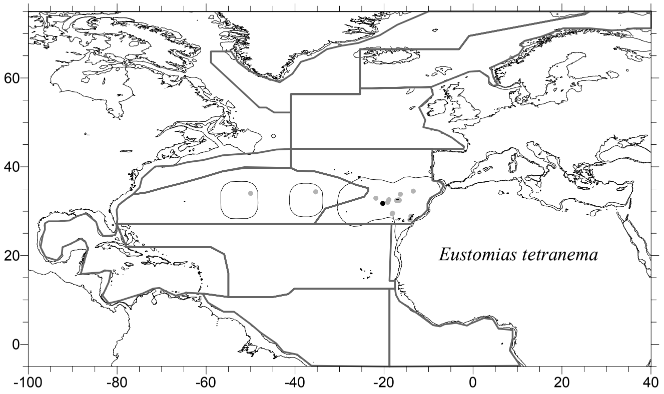


Fig. F82. *Eustomias tetranema* (30): Subtropical (east).

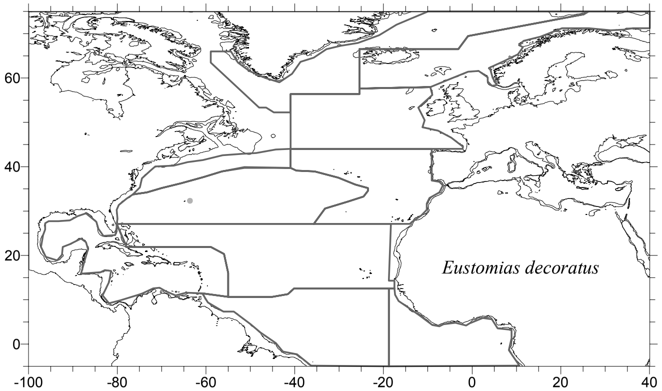


Fig. F83. *Eustomias decoratus* (1): Subtropical (west); North Atlantic endemic.

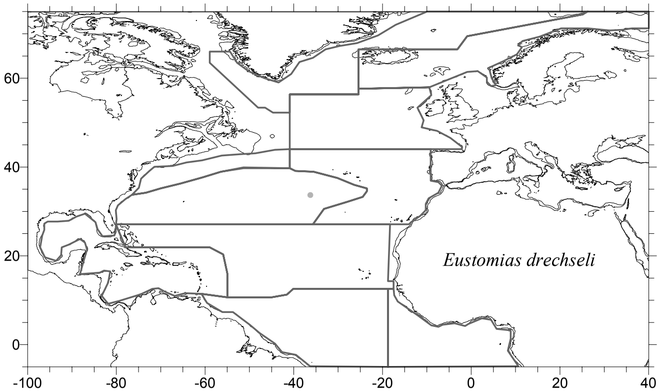


Fig. F84. *Eustomias drechseli* (1): Subtropical (west); North Atlantic endemic.

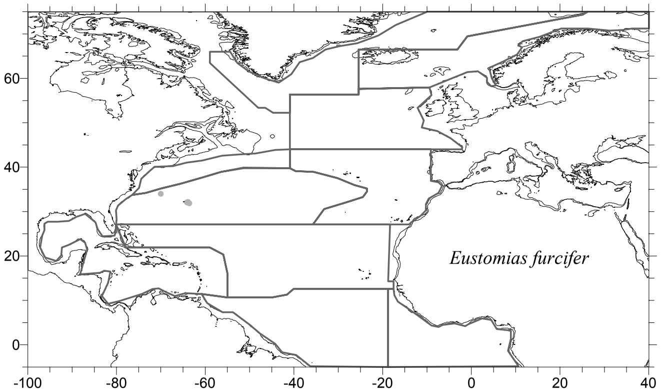


Fig. F85. *Eustomias furcifer* (7): Subtropical (west).

Eustomias (*Neostomias*; *Triclonostomias*)

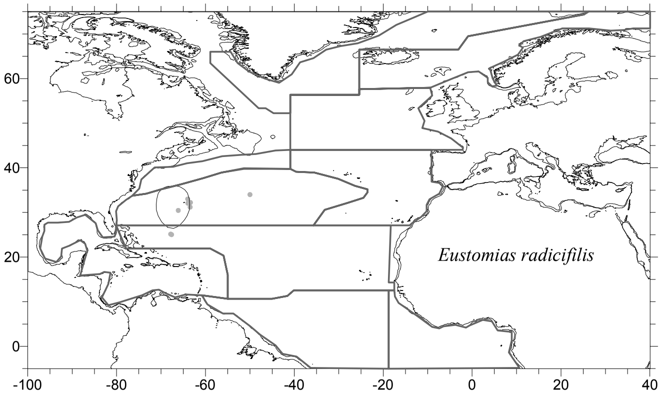


Fig. F86. *Eustomias radicifilis* (13): Subtropical (west); North Atlantic endemic.

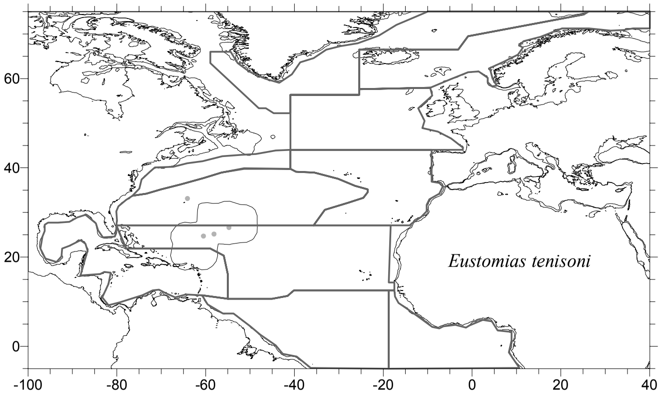


Fig. F87. *Eustomias tenisoni* (6): Western Tropical Gyre.

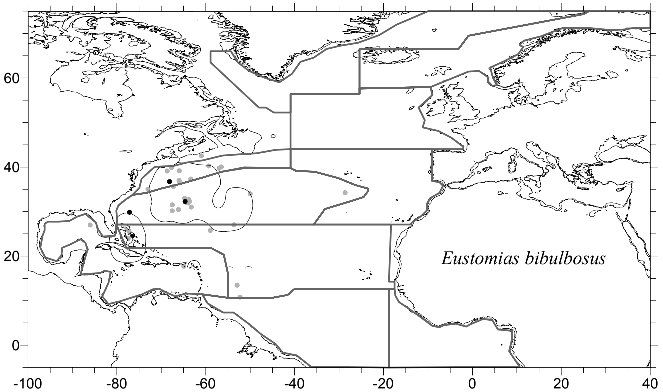


Fig. F88. *Eustomias bibulbosus* (60): Subtropical (west); North Atlantic endemic.

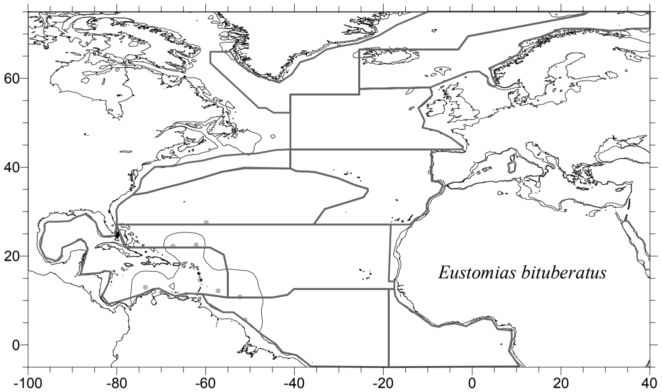


Fig. F89. *Eustomias bituberatus* (10): Caribbean (distant neritic); North Atlantic endemic.

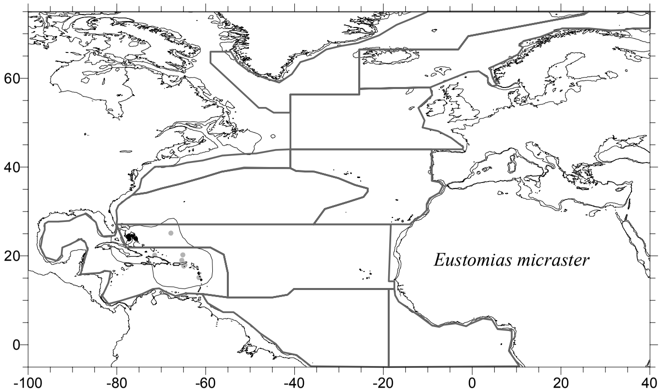


Fig. F90. *Eustomias micraster* (10): Caribbean (distant neritic); North Atlantic endemic.

Eustomias (*Triclonostomias; Nominostomias* I)

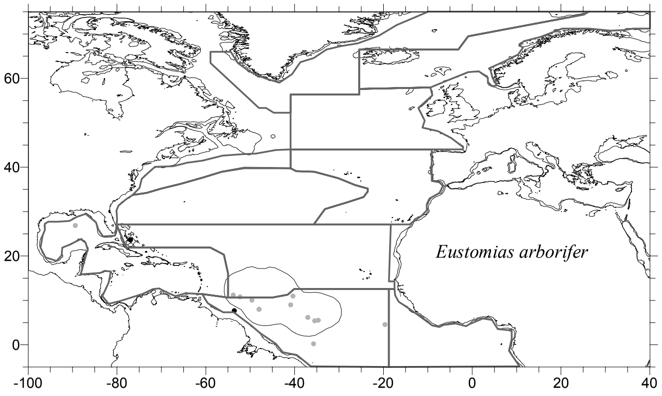


Fig. F91. *Eustomias arborifer* (18): Equatorial (west).

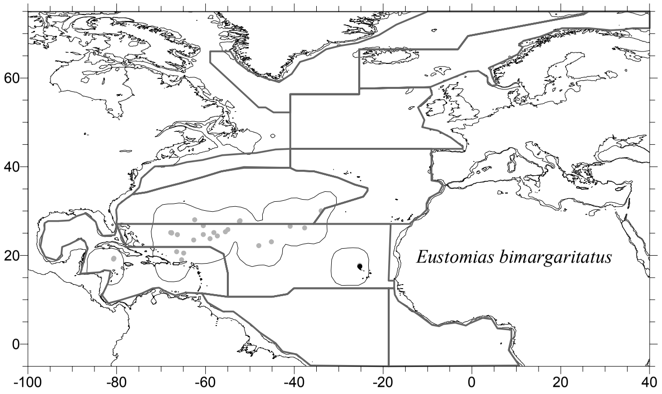


Fig. F92. *Eustomias bimargaritatus* (31): Western Tropical Gyre complex; Tropical Gyre - Caribbean; North Atlantic endemic.

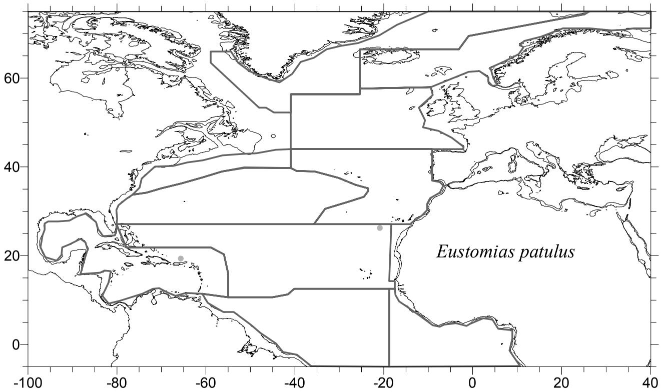


Fig. F93. *Eustomias patulus* (2): Eastern Tropical - Equatorial; Eastern Tropical; limited range (distant neritic); North Atlantic endemic.

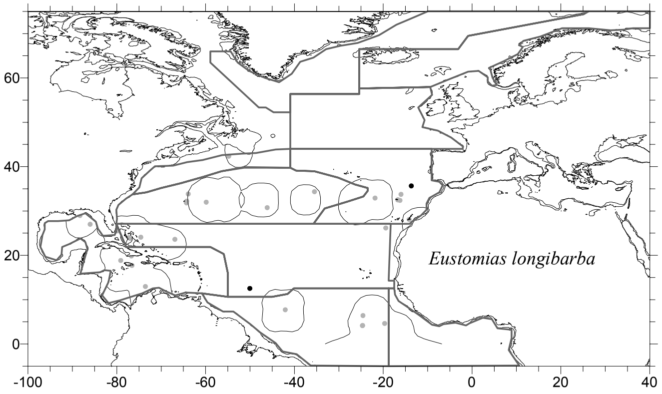


Fig. F94. *Eustomias longibarba* (36): Equatorial complex; Equatorial (west) / Caribbean / Subtropical.

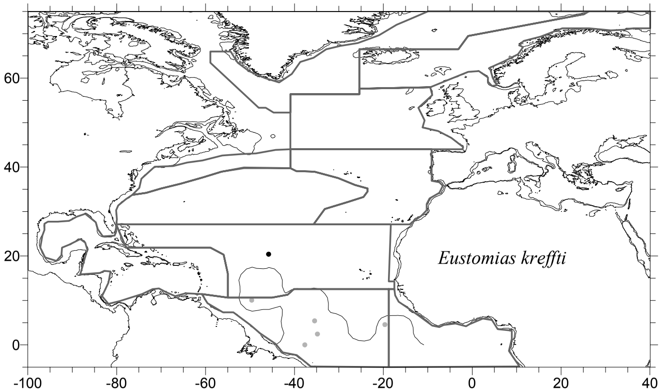


Fig. F95. *Eustomias kreffti* (5): Equatorial (west).

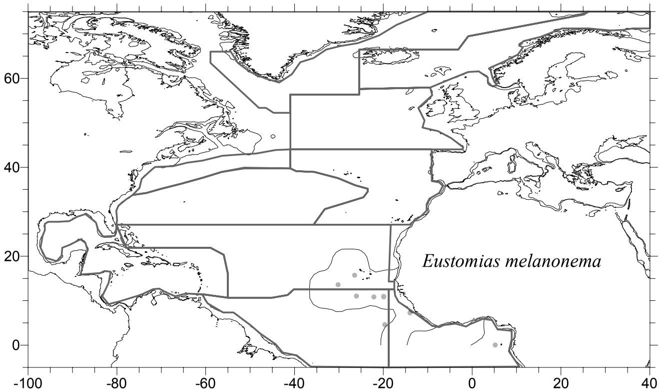


Fig. F96. *Eustomias melanonema* (11): Eastern Tropical – Equatorial (east); limited range (distant neritic).

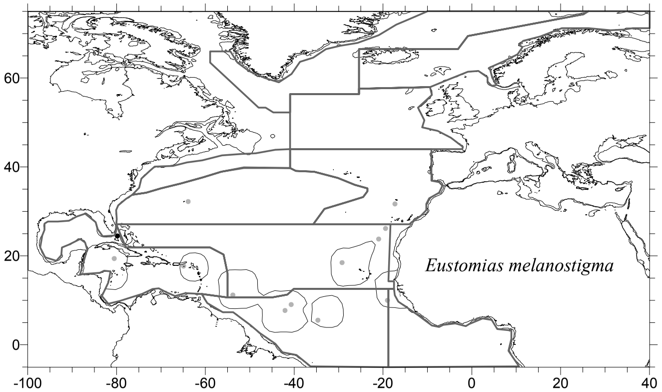


Fig. F97. *Eustomias melanostigma* (14): Equatorial (west) - Eastern Tropical – Caribbean.

Eustomias (*Nominostomias* II, IV, V, III)

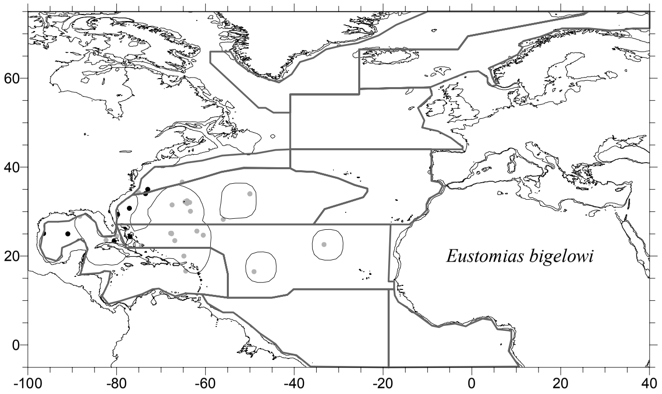


Fig. F98. *Eustomias bigelowi* (41): Western Tropical Gyre complex; Tropical Gyre - Subtropical (west).

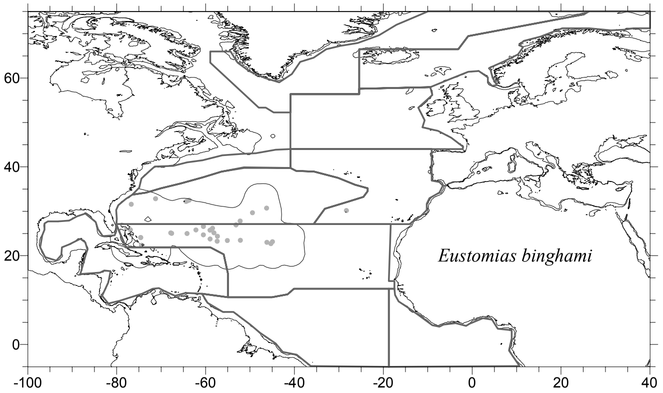


Fig. F99. *Eustomias binghami* (54): Western Tropical Gyre; North Atlantic endemic.

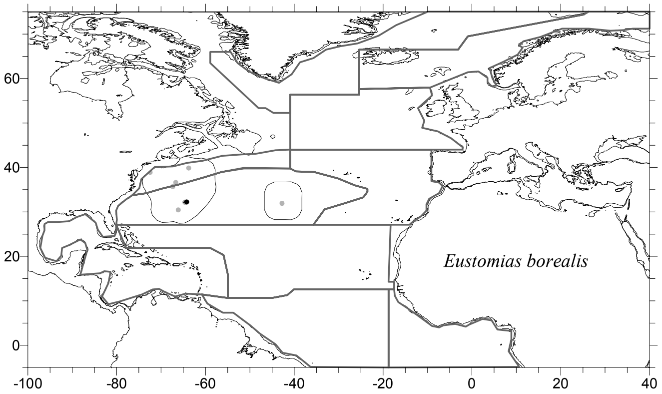


Fig. F100. *Eustomias borealis* (9): Subtropical (west); North Atlantic endemic.

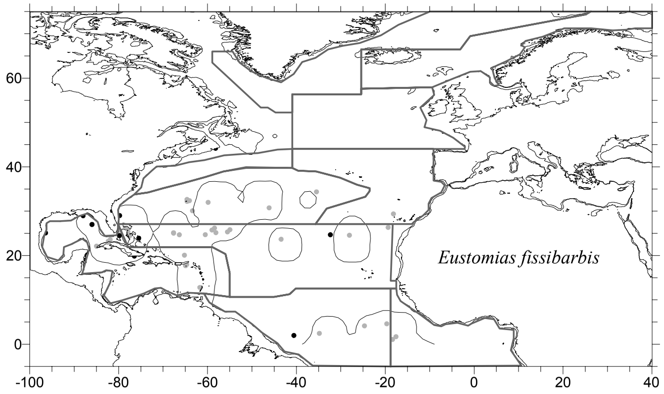


Fig. F101. *Eustomias fissibarbis* (50): Tropical - Equatorial; Northern Tropical - Caribbean / Equatorial.

Eustomias (*Dinematochirus*)

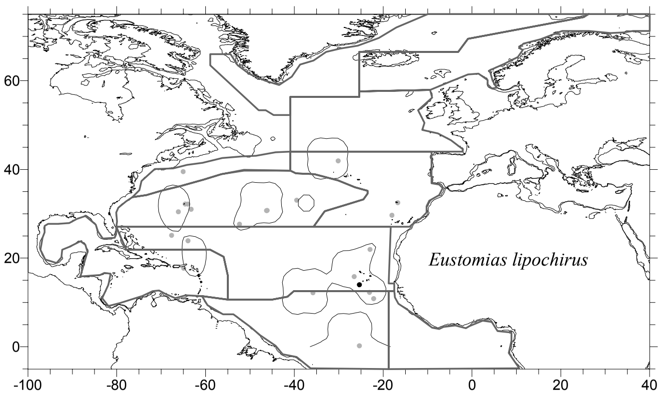


Fig. F102. *Eustomias lipochirus* (28): Equatorial complex; Equatorial (east) - Eastern tropical / Subtropical (west).

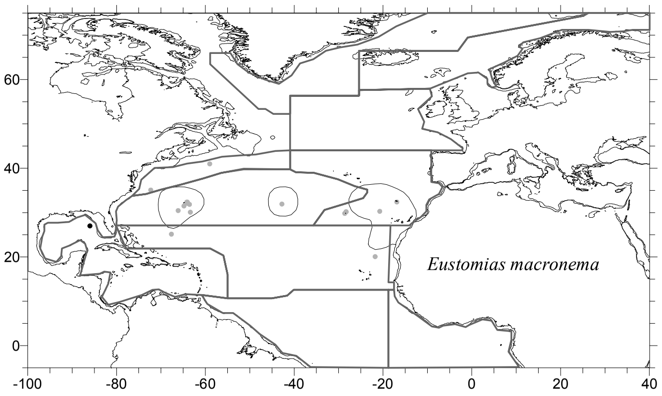


Fig. F103. *Eustomias macronema* (23): Subtropical.

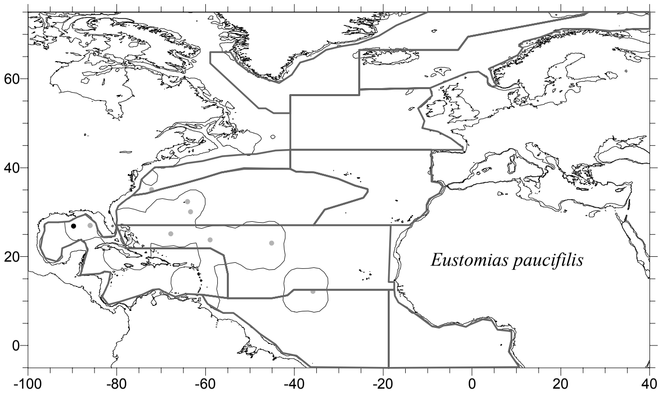


Fig. F104. *Eustomias paucifilis* (17): Caribbean complex; Caribbean - Tropical Gyre; North Atlantic endemic.

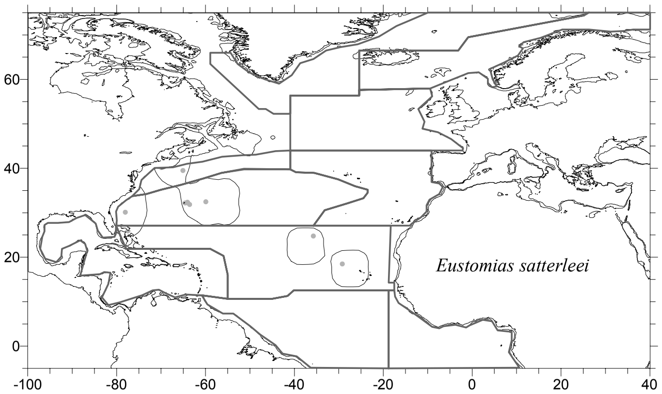


Fig. F105. *Eustomias satterleei* (14): Subtropical (west).

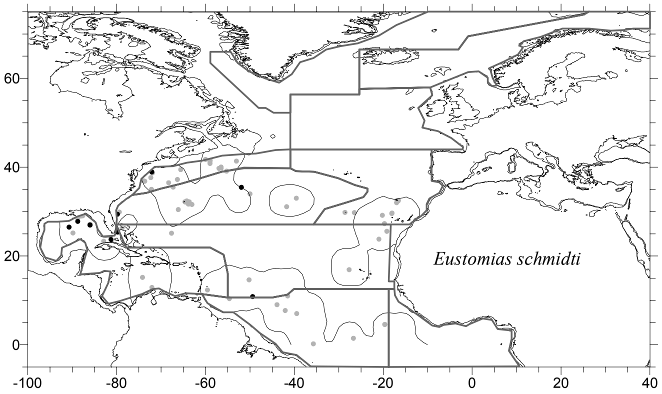


Fig. F106. *Eustomias schmidti* (125): Caribbean complex; Caribbean - Equatorial (west) – Subtropical.

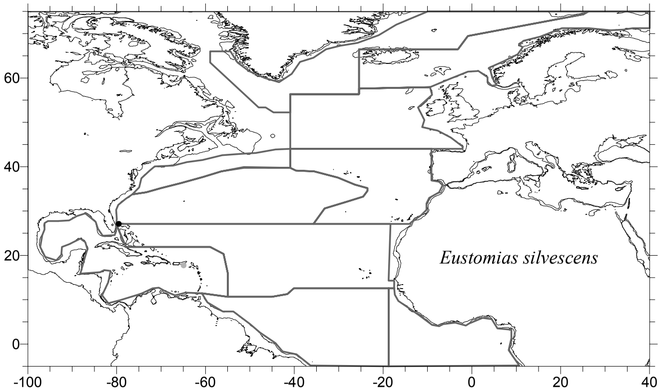


Fig. F107. *Eustomias silvescens* (1): Caribbean (distant neritic); North Atlantic endemic.

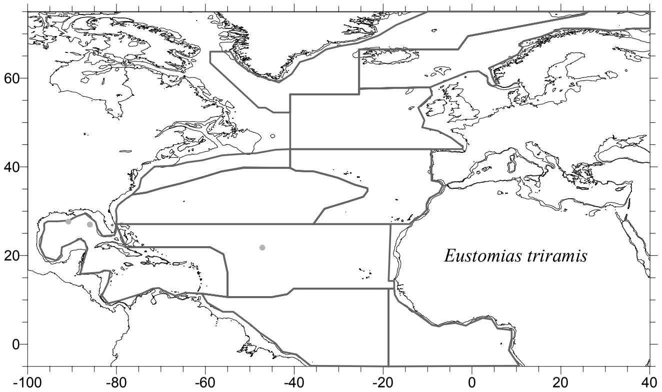


Fig. F108. *Eustomias triramis* (4): Caribbean complex; Caribbean - tropical (west) (distant neritic); North Atlantic endemic.

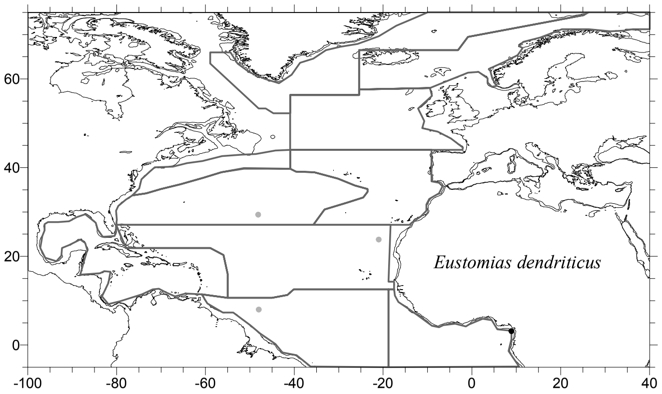


Fig. F109. *Eustomias dendriticus* (3): Equatorial complex; Equatorial (west) / Eastern tropical / Subtropical (west); North Atlantic endemic.

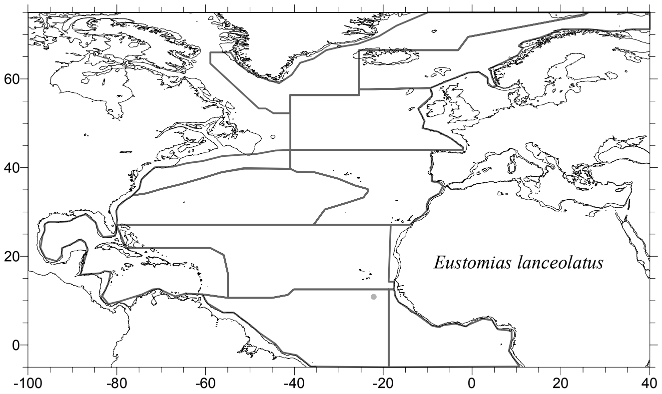


Fig. F110. *Eustomias lanceolatus* (1): Eastern Tropical - Equatorial; Equatorial (east).

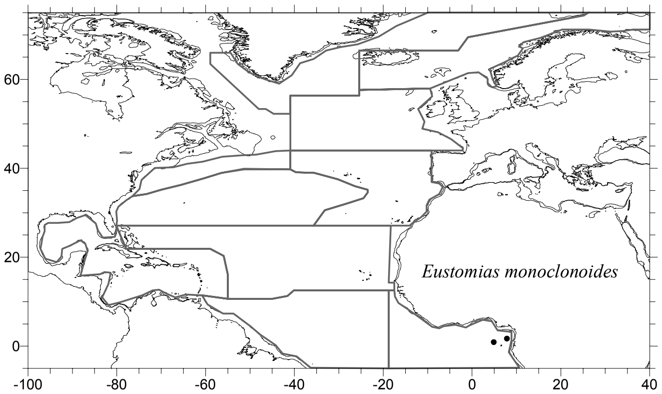


Fig. F111. *Eustomias monoclonoides* (0): Eastern Tropical - Equatorial; Equatorial (east).

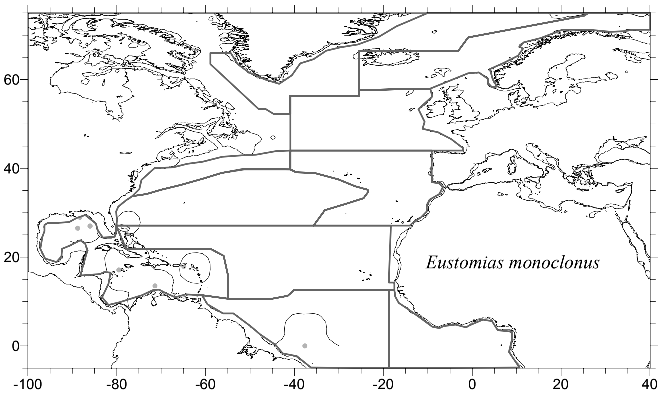


Fig. F112. *Eustomias monoclonus* (10): Caribbean (distant neritic).

Eustomias (*Dinematochirus*; *E. dendriticus*)

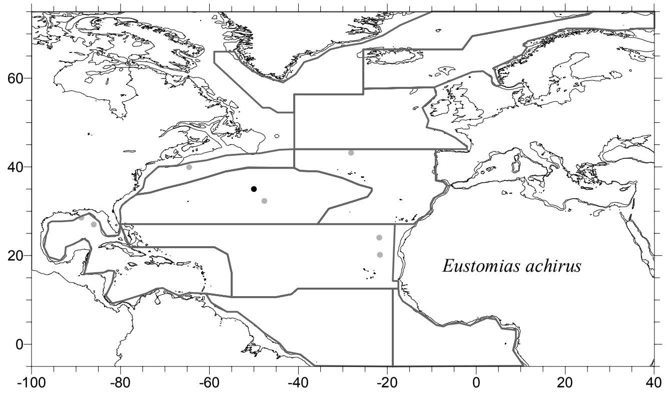


Fig. F113. *Eustomias achirus* (7): Eastern Tropical complex; Eastern tropical / Subtropical (west).

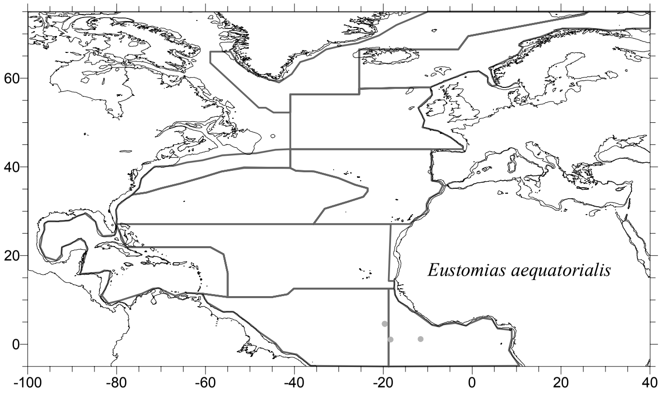


Fig. F114. *Eustomias aequatorialis* (7): Eastern Tropical - Equatorial; Equatorial (east).

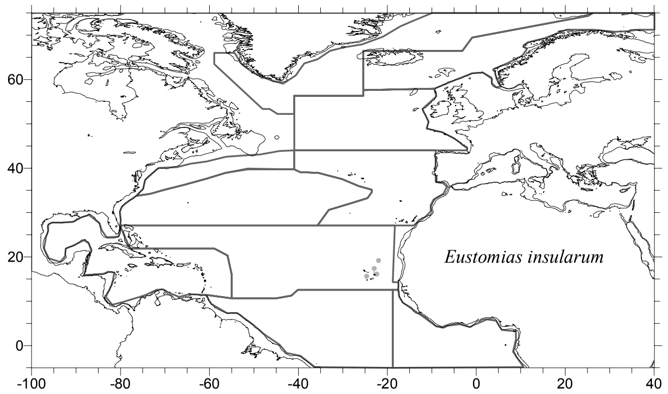


Fig. F115. *Eustomias insularum* (4): Eastern Tropical - Equatorial; Eastern Tropical; limited range (distant neritic); North Atlantic endemic.

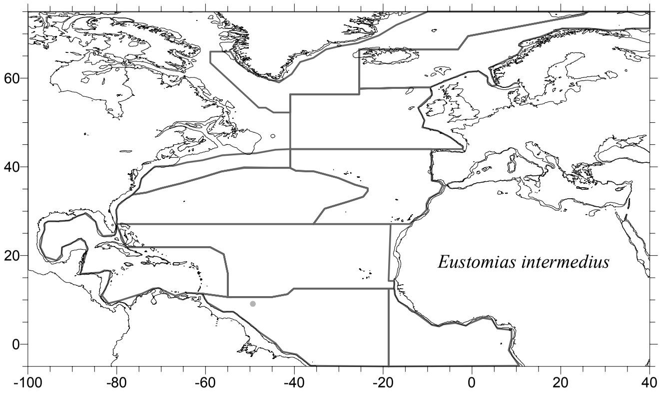


Fig. F116. *Eustomias intermedius* (1): Equatorial (west).

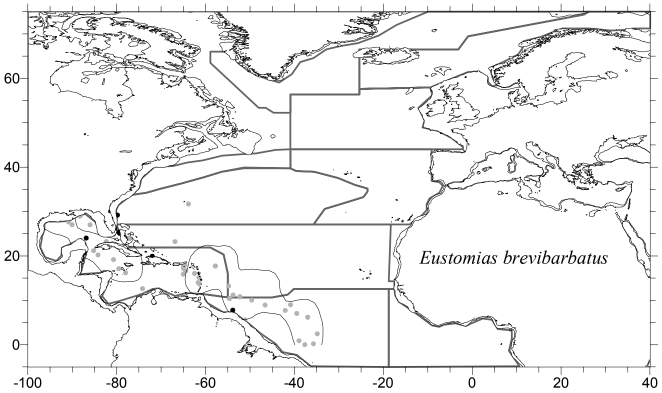


Fig. F117. *Eustomias brevibarbatus* (58): Equatorial (west) - Caribbean (distant neritic).

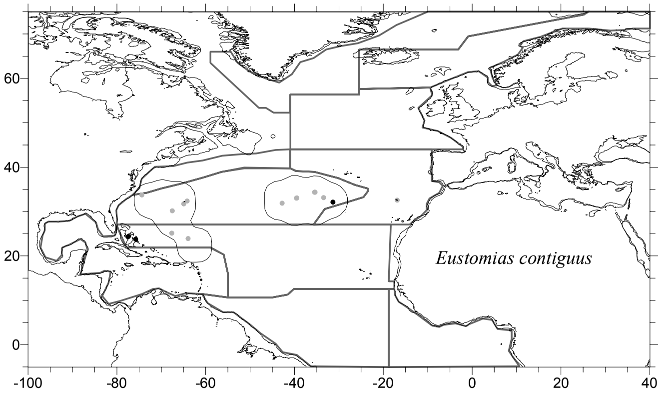


Fig. F118. *Eustomias contiguus* (15): Subtropical (west); North Atlantic endemic.

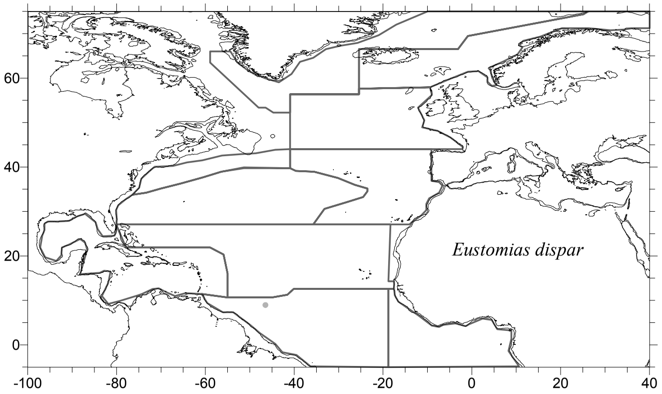


Fig. F119. *Eustomias dispar* (1): Equatorial (west); North Atlantic endemic.

Eustomias (*Dinematochirus*; *E. achirus*; *Biradiostomas* I)

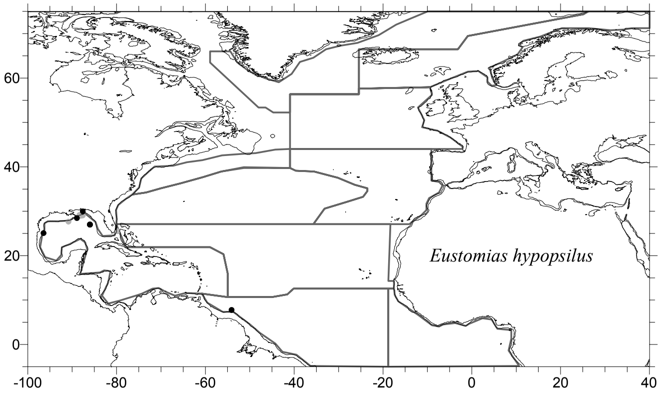


Fig. F120. *Eustomias hypopsilus* (35): Caribbean (distant neritic); North Atlantic endemic.

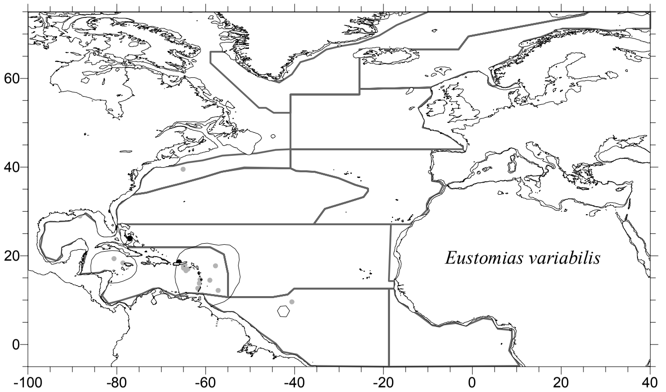


Fig. F121. *Eustomias variabilis* (30): Caribbean (distant neritic); North Atlantic endemic.

Eustomias (*Biradiostomias* I; II)

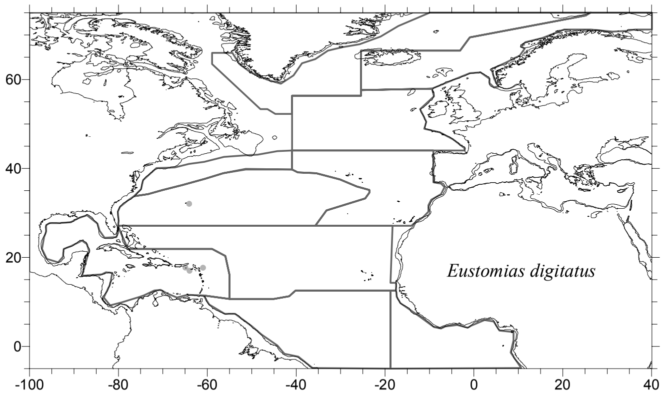


Fig. F122. *Eustomias digitatus* (4): Caribbean (distant neritic); North Atlantic endemic.

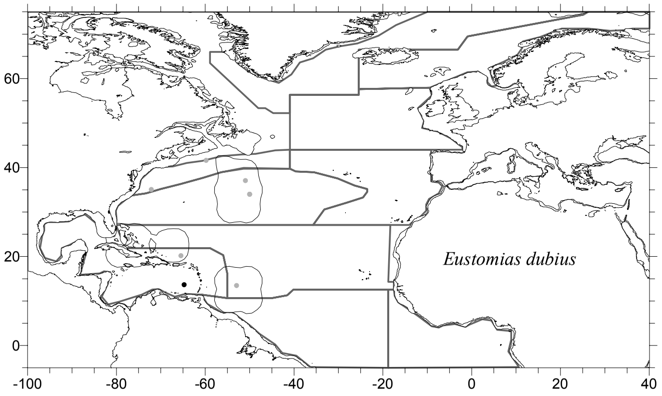


Fig. F123. *Eustomias dubius* (8): Caribbean complex; Caribbean / Subtropical (west); North Atlantic endemic.

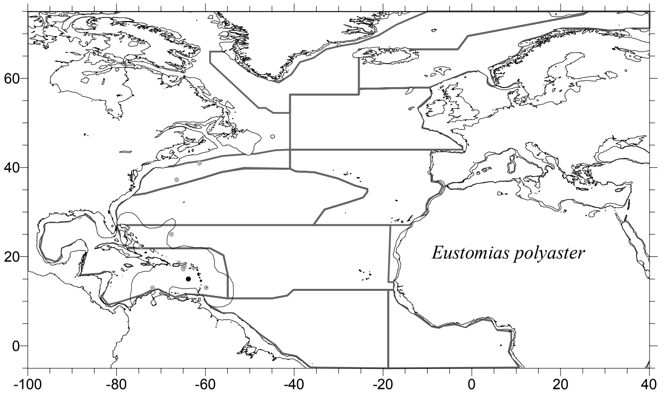


Fig. F124. *Eustomias polyaster* (16): Caribbean (distant neritic); North Atlantic endemic.

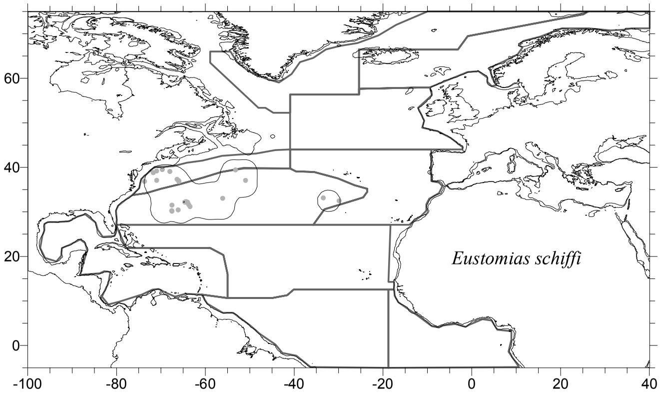


Fig. F125. *Eustomias schiffi* (27): Subtropical (west); North Atlantic endemic.

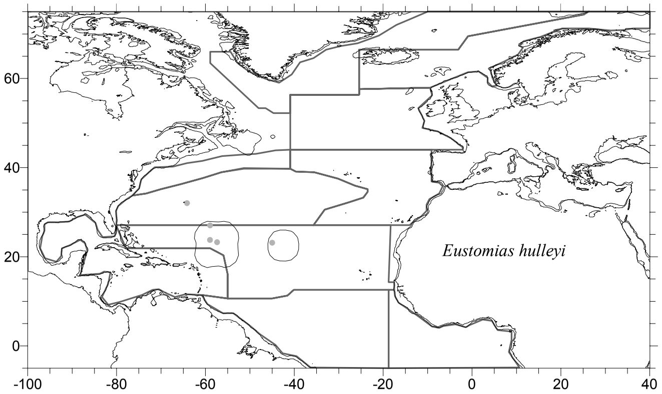


Fig. F126. *Eustomias hulleyi* (11): Western Tropical Gyre; North Atlantic endemic.

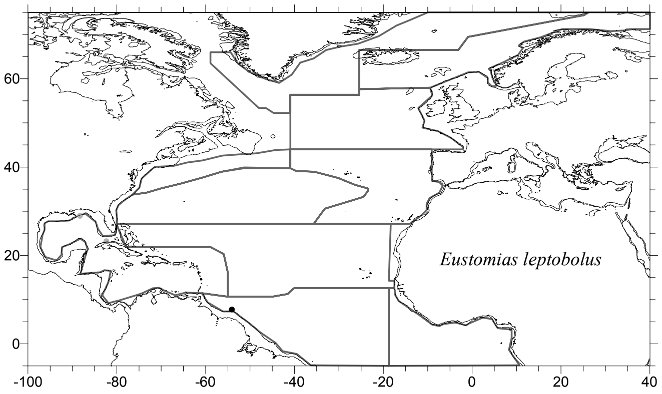


Fig. F127. *Eustomias leptobolus* (2): Caribbean (distant neritic); North Atlantic endemic.

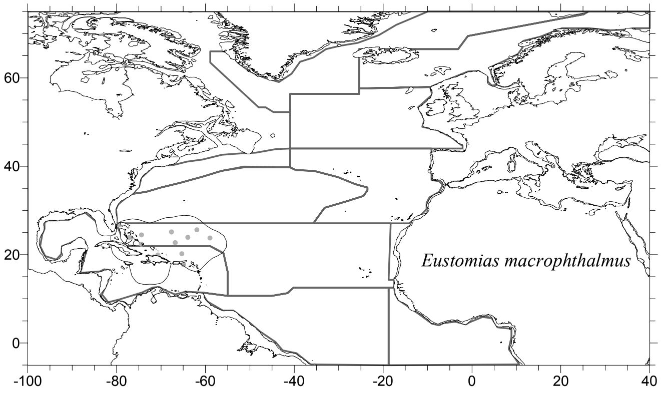


Fig. F128. *Eustomias macrophthalmus* (13): Western Tropical Gyre complex; Tropical Gyre - Caribbean; North Atlantic endemic.

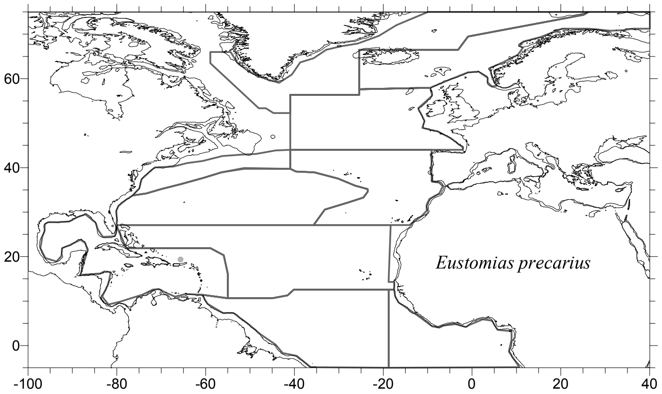


Fig. F129. *Eustomias precarius* (1): Caribbean (distant neritic); North Atlantic endemic.

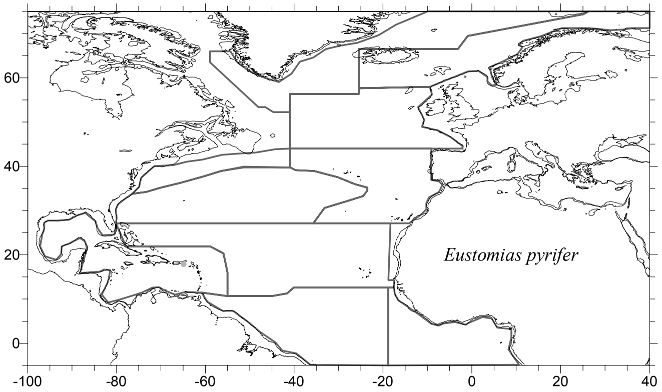


Fig. F130. *Eustomias pyrifer* (1): Caribbean (distant neritic); North Atlantic endemic.

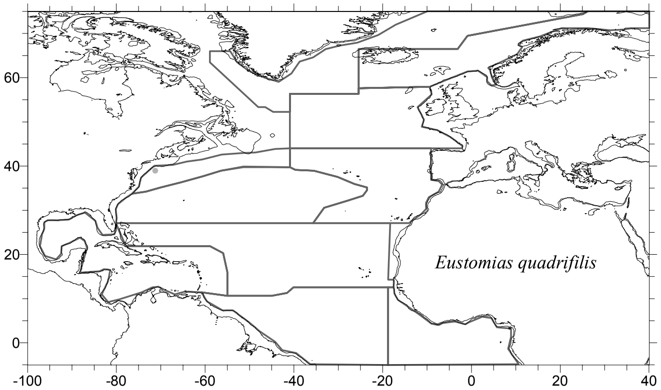


Fig. F131. *Eustomias quadrifilis* (1): Boreal (west); North Atlantic endemic.

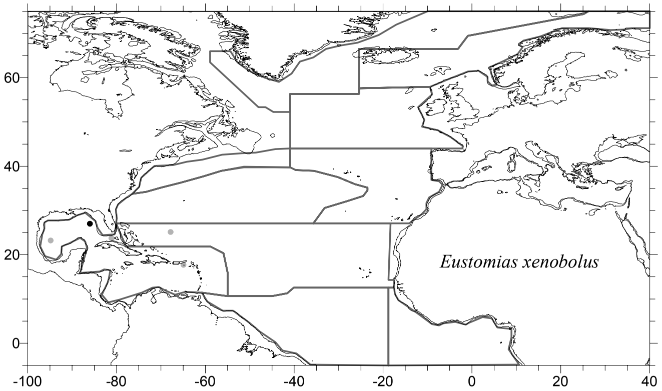


Fig. F132. *Eustomias xenobolus* (4): Caribbean (distant neritic); North Atlantic endemic.

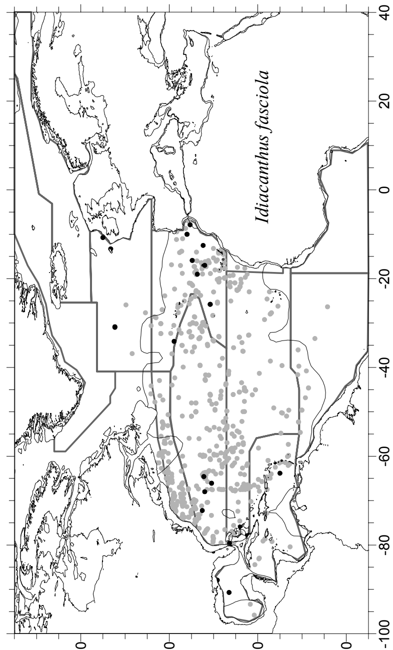


Fig. F133. *Idiacanthus fasciola* (1879): Tropical – Subtropical.

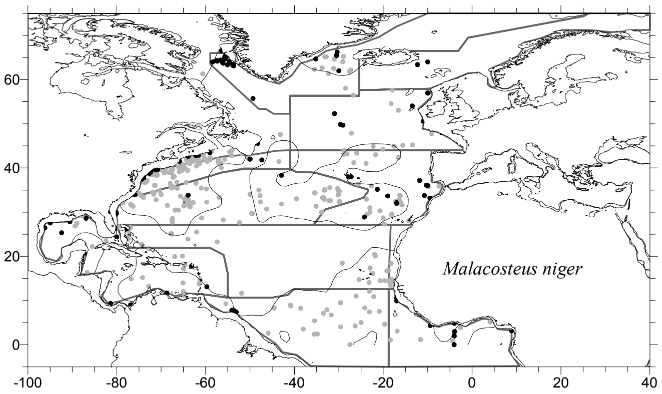


Fig. F134. *Malacosteus niger* (896): Widespread (anti-central).

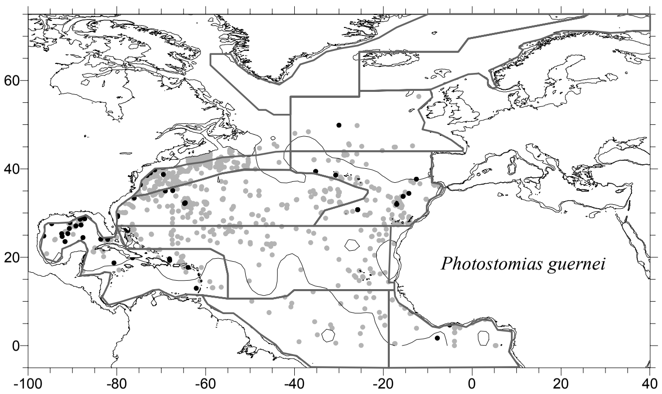


Fig. F135. *Photostomias guernei* (2978): Uncertain pattern.

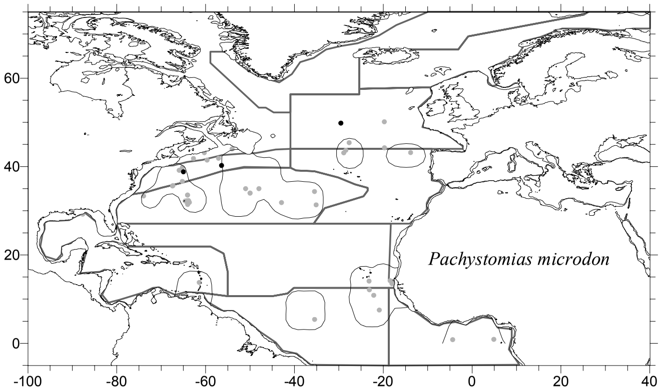


Fig. F136. *Pachystomias microdon* (60): Equatorial complex; Equatorial (east) – Eastern tropical / Subtropical (west).

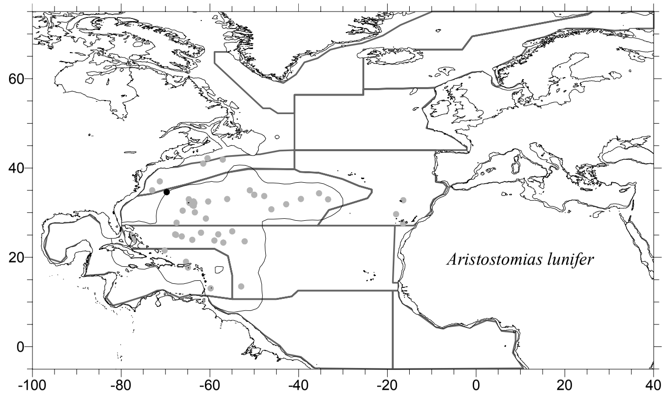


Fig. F137. *Aristostomias lunifer* (74): Western Tropical Gyre complex; Tropical Gyre - Caribbean - Subtropical (west).

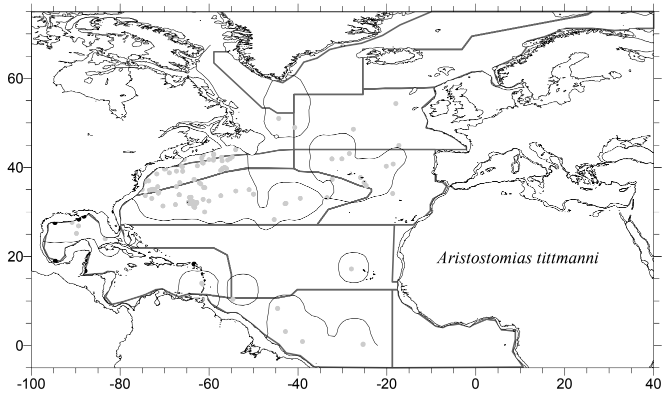


Fig. F138. *Aristostomias tittmanni* (179): Subtropical complex; Subtropical (west) - Boreal (west) / Equatorial (west).

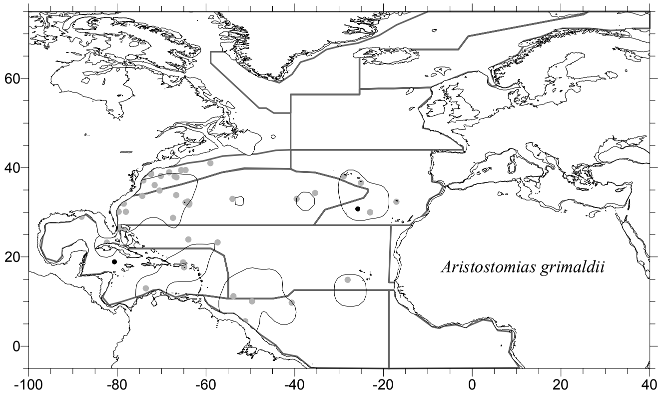


Fig. F139. *Aristostomias grimaldii* (54): Subtropical complex; Subtropical (west) - Caribbean - Equatorial (west).

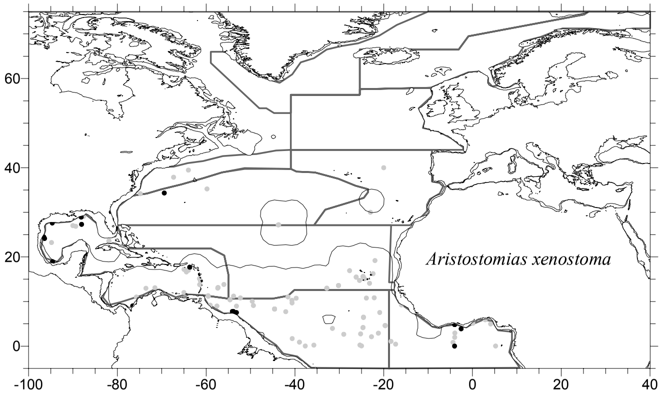


Fig. F140. *Aristostomias xenostoma* (174): Equatorial; Eastern Tropical – Caribbean.

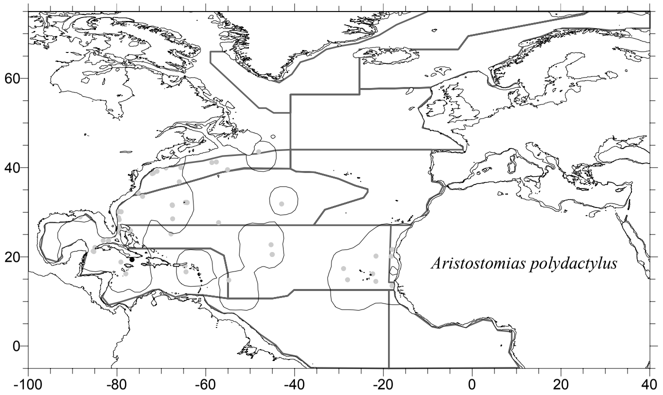


Fig. F141. *Aristostomias polydactylus* (64): Amphi-Atlantic (distant neritic); Tropical.

Appendix G

Biodiversity characterization of North Atlantic Longhurst's Provinces

This appendix provides biodiversity information concerning the stomiid faunas from the North Atlantic Longhurst's Provinces. The information compiled is discussed in Chapter 7. The entire sample of North Atlantic stomiid fish by species is summarised in Table G.1.

Methods

Species-areas and rarefaction curves

Two saturation curves were computed for each province. The species-area curve shows the cumulative numbers of different species as new samples are added. The samples were accumulated at a random order and the curve represents an average of 999 permutations. It is assumed that a species-area curve that reaches an asymptote as more samples are incorporated indicates a good coverage of the fauna under study. The net-haul (*field_code*) was the sampling unit used to produce the species-area plots presented.

The classical rarefaction formula is widely used in diversity studies as it generates the expected number of species (ES[n]) by reducing to a standard size, samples of different sizes. Thus it is an index of species richness and allows comparisons between two or more "communities" that were differently sampled. It is expected that a rarefaction curve reach an asymptote as more specimens are added to the sample. Its actual phase, when numbers equal those obtained from sampling, indicates how satisfactory surveyed a province was. Moreover, the more diverse a province is the more elevated is the curve.

Species-abundance distributions

Two types of relative species-abundances plots were computed for every province: the abundance-biomass curve (ABC) and the geometric class plot. Both extract information about species abundances. The ABC plots were based on the ranking of species in decreasing order of abundance and biomass (dominance) expressed as the percentage of the total abundance of all species. The axis of species ranks was log transformed and the relative abundance of species cumulated. These k-dominance curves have an advantage that they compare abundances and biomasses in the same view. The spatial relationship between the abundances and biomass curves distributions among species is thought to reflect, for at least some taxonomic groups (of the benthic macrofauna), the level of disturbance the assemblage of species faces (originally pollution; Clarke & Warwick, 1994). The biomass curve lies below the abundance curve under disturbance and the opposite for non- affected communities. Both curves overlap for moderated disturbed conditions. Based on the relative position of the abundance and biomass curves, the authors created a W statistics that takes values in the range (-1, 1), being positive when the sample is biomass dominated ("undisturbed") and vice-versa.

The plots of geometric abundances classes represent the dominance structure of the community. Class 1 includes (in percentage) the species represented only by one specimen; class 2 by species with 2-3 individuals; class 3 by 4-7; class 4 by 8-15, class 5, 16-31; etc. The geometric plots were computed on the matrices of numbers species per Longhurst provinces.

Taxonomic funnels

These are randomised statistical procedure, developed by Clarke & Warwick (2001) that intend to test the probability of a sample to be drawn from a background "master" list that characterizes the faunistic composition of a (biogeographic) region. The test computes the average taxonomic distinctness (Δ+) and the variation in taxonomic distinctness (Λ+) (see methods in Chapter 7) drawn from a "taxonomic" tree of the regional species inventory. Because Δ+ and Λ+ are independent of sampling size (effort) they are therefore useful to compare samples with different number of species (and specimens), against a master list of regional fauna. The funnel is shaped by the 95% limits of the statistics probability distributions for a range of sub-(regional) lists, and therefore accommodates samples with different number of species. The indices Δ+ and Λ+ were computed for each *sq_5x5* and plotted against the expected 95% funnels obtained from the respective provincial (*Lgh_P*) faunal list.

Diversity indices

Regional and local diversity indices were computed for each province (see Chapter 7 for methods). S: number of species; H’: Shannon-Wiener diversity (base e); J’: Pielou’s evenness; d: species richness (Margalef); 1-λ’: Simpson’s dominance; N1 - N∞: Hill’s numbers; Δ: Taxonomic diversity; SΔ+: total taxonomic distinctness; Φ: average phylogenetic diversity; SΦ+: total phylogenetic diversity. For the local diversity (computed for each sq_5x5 and then averaged per Longhurst provinces) the following statistics were computed (grey cells): mean, 95% significance limits range; maximum and minimum.

Typical species assemblages

Clarke and Warwick (1994) described a method based on the average Bray-Curtis dissimilarity between pairs of samples, to detect discriminator species between groups of samples, or typical species within a group of samples. The contribution from each species is obtained by breaking the average dissimilarity values between samples; standard deviation measures the consistency of those contributions. The method is available in PRIMER package (SIMPER: similarity percentage) and was used to identify the contribution a species makes to the average similarity between samples (field_code) within a province. A typical species is recurrently abundant throughout the samples and shows low similarity standard deviation. Computations were performed on matrices of number of specimens per species per sq_5x5 for each province. Data were standardised and fourth root transformed. The cut-off percentage of higher-contributing species was 90% for assemblages with more than 10 species (see SIMPER Tables).

ETRA – Eastern Tropical Atlantic Province

Table G.1.1 Basic data (ETRA) (see methods for explanations)

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
10+1	106	284	2026.5	728	33	17

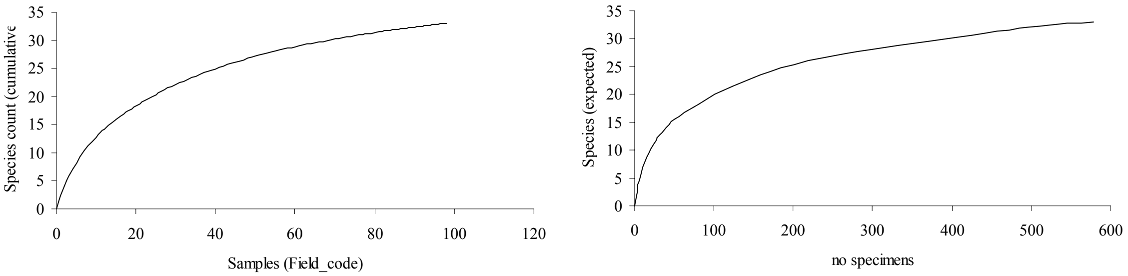


Figure G.1.1 Saturation curves (ETRA); a) species samples plot; b) rarefaction.

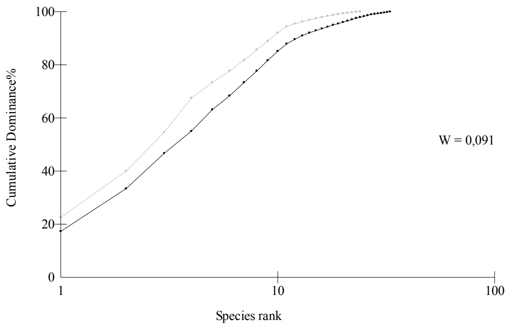


Figure G.1.2 Abundance-Biomass Curve (ETRA). Grey: biomass; black: abundance.

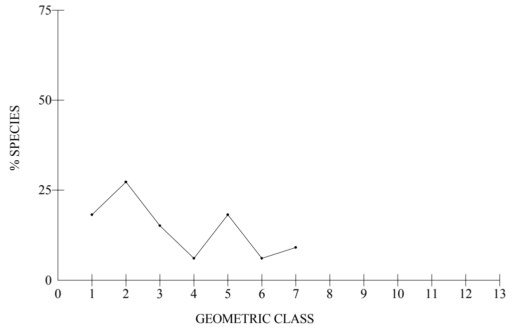


Figure G.1.3 Geometric plot (ETRA).

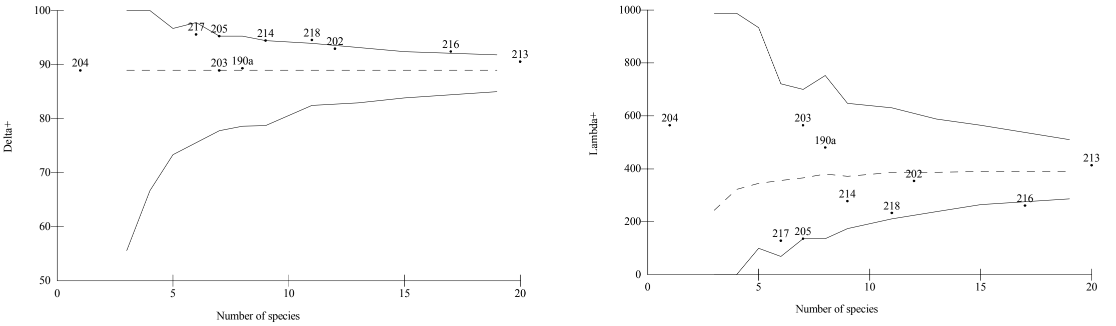


Figure G.1.4 Taxonomic funnels (ETRA); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.1.2 Regional and averaged local (grey) biodiversity indices (ETRA) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	33	9.55	2.66	0.76	0.93	14.33	10.13	5.78	89.0	393.5	55.6
mean	9.80	2.90	1.82	0.80	0.81	5.96	4.66	2.94	92.6	316.4	78.2
-95.0%	5.86	1.73	1.54	0.68	0.70	3.92	3.16	2.13	90.7	201.6	69.8
95.0%	13.74	4.08	2.09	0.92	0.92	8.00	6.16	3.76	94.6	431.3	86.7
min	1.00	1.45	1.12	0.51	0.46	1.00	1.00	1.00	88.9	128.4	60.0
max	20.00	5.78	2.49	0.98	0.97	12.01	8.28	4.50	95.6	564.4	100.0
n	10	9	9	9	9	10	10	10	9	9	10

Table G.1.3 Typical stomiid species assemblage (ETRA); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Photostomias guernei	Uncertain pattern	4.7	5.4	1.1	18.4	18.4
Stomias affinis	Amphi-Atlantic (distant neritic)	10.0	4.6	0.9	15.4	33.7
Borostomias elucens	Eastern Tropical - Equatorial	2.3	2.8	0.7	9.5	43.3
Chauliodus schmidti	Eastern Tropical - Equatorial	7.7	2.8	0.6	9.4	52.7
Aristostomias xenostoma	Equatorial	2.5	2.5	0.7	8.4	61.0
Chauliodus sloani	Widespread (anti-central)	2.9	2.3	0.5	7.7	68.7
OdontoStomias micropogon	Eastern Tropical - Equatorial	1.6	1.7	0.5	5.6	74.3
Stomias lampropeltis	Eastern Tropical - Equatorial	9.3	1.2	0.4	4.0	78.3
Stomias boa boa	Mediterranean - Eastern Tropical	1.0	1.1	0.4	3.5	81.8
Malacosteus niger	Widespread (anti-central)	2.0	1.0	0.4	3.5	85.3
Astronesthes micropogon	Amphi-Atlantic (distant neritic)	0.6	0.7	0.4	2.2	87.5
Astronesthes richardsoni	Equatorial	3.0	0.6	0.3	2.0	89.5

Other species: *Astronesthes macropogon; Astronesthes caulophorus; Stomias longibarbatus; Flagellostomias boureei; Eustomias macrurus; Astronesthes niger; Eustomias melanonema; Eustomias aequatorialis; Borostomias mononema; Pachystomias microdon; Melanostomias melanops*.

WTRA – Western Tropical Atlantic Province

Table G.2.1 Basic data (WTRA) (see methods for explanations)

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
13+11	229	1004	6101.0	2849	83	22

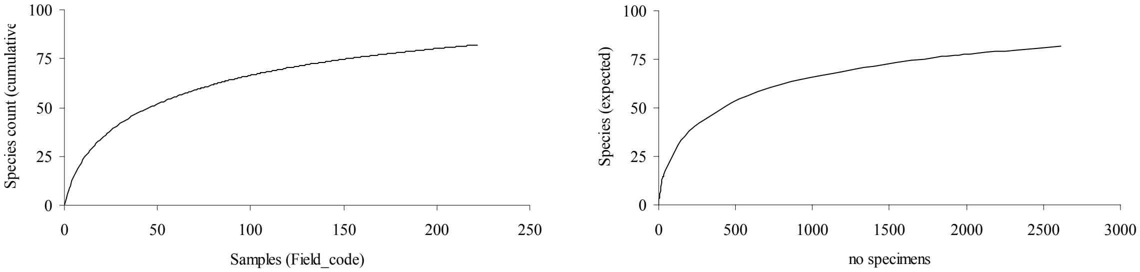


Figure G.2.1. Saturation curves (WTRA); a) species samples plot; b) rarefaction.

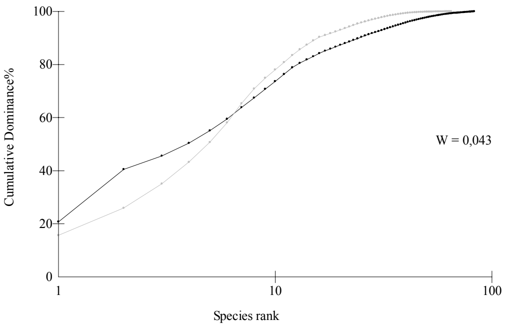


Figure G.2.2 Abundance-Biomass Curve (WTRA). Grey: biomass; black: abundance.

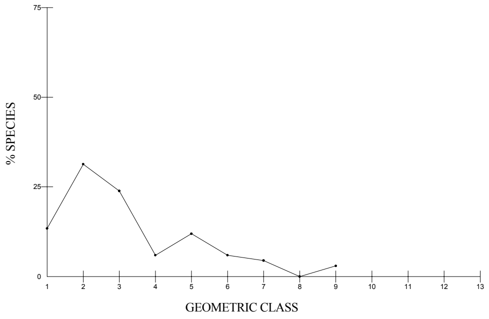


Figure G.2.3 Geometric plot. (WTRA)

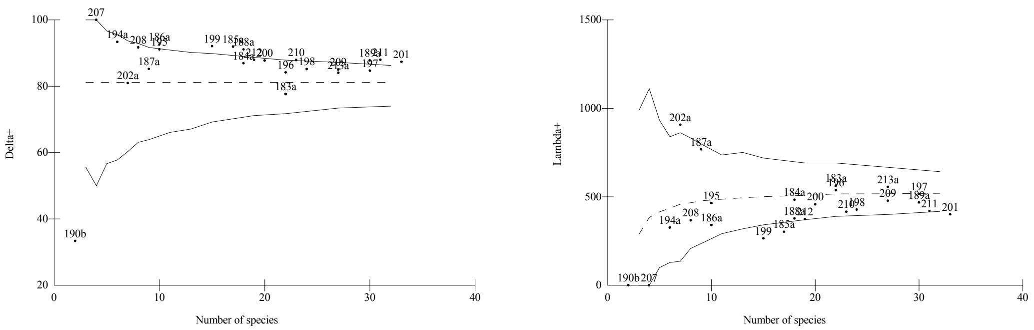


Figure G.2.4 Taxonomic funnels (WTRA). a) average taxonomic distinctness (Δ^{+}); b) variation in taxonomic distinctness (Λ^{+}); numbers represents *sq_5x5* identification

Table G.2.2 Regional and averaged local (grey) biodiversity indices (WTRA) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	83	21.82	3.01	0.68	0.92	20.29	10.09	4.81	81.1	522.7	44.6
mean	18.04	4.59	2.04	0.76	0.80	9.06	6.10	3.18	85.7	463.5	65.6
-95.0%	14.10	3.52	1.77	0.70	0.74	7.04	4.67	2.58	80.6	398.6	61.0
95.0%	21.98	5.66	2.30	0.82	0.86	11.08	7.52	3.79	90.8	528.5	70.2
min	2.00	0.46	0.67	0.46	0.44	1.96	1.77	1.37	33.3	265.1	54.8
max	33.00	9.46	2.84	0.97	0.95	17.09	13.55	7.40	100.0	907.0	100.0
n	24	24	24	24	24	24	24	24	24	22	24

Table G.2.3 Typical stomiid species assemblage (WTRA); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus sloani	Widespread (anti-central)	21.5	6.6	1.5	17.9	17.9
Astronesthes richardsoni	Equatorial	22.6	5.7	1.3	15.5	33.4
Stomias affinis	Amphi-Atlantic (distant neritic)	4.8	2.6	0.8	7.0	40.3
Thysanactis dentex	Equatorial	5.3	2.4	0.8	6.4	46.7
Heterophotus ophistoma	Equatorial	4.8	2.2	0.9	6.1	52.8
Astronesthes atlanticus	Equatorial	5.5	2.1	0.8	5.8	58.6
Aristostomias xenostoma	Equatorial	2.9	2.0	0.8	5.5	64.1

Malacosteus niger	Widespread (anti-central)	5.1	1.7	0.6	4.5	68.6
Photostomias guernei	Uncertain pattern	2.8	1.5	0.7	4.0	72.5
Bathophilus pawneei	Caribbean complex	1.8	1.2	0.6	3.4	75.9
Eustomias enbarbatus	Equatorial complex	1.4	1.0	0.6	2.7	78.6
Astronesthes niger	Uncertain pattern	3.9	0.9	0.4	2.6	81.1
Eustomias macrurus	Equatorial	1.3	0.6	0.5	1.7	82.8
Melanostomias tentaculatus	Tropical - Equatorial	0.7	0.6	0.4	1.6	84.4
Borostomias elucens	Eastern Tropical - Equatorial	3.2	0.5	0.4	1.4	85.8
Chauliodus schmidti	Eastern Tropical - Equatorial	3.6	0.5	0.3	1.3	87.2
Eustomias arborifer	Equatorial	0.6	0.5	0.4	1.2	88.4
Idiacanthus fasciola	Tropical - Subtropical	0.8	0.4	0.3	1.2	89.6

Other species: *Eustomias brevibarbatus; Stomias longibarbatus; Echiostoma barbatum; Melanostomias biseriatus; Astronesthes gemmifer; Astronesthes micropogon; Flagellostomias boureei; Melanostomias melanops; Eustomias schmidti; Aristostomias tittmani; Leptostomias gracilis; Photonectes mirabilis; Bathophilus nigerrimus; Eustomias kreffti; Stomias lampropeltis; Eustomias melanonema; Eustomias obscurus; Eustomias melanostigma; Photonectes phyllopogon; Eustomias longibarba; Astronesthes similis; Aristostomias grimaldii; Astronesthes caulophorus; Melanostomias macrophotus; Leptostomias bermudensis; Eustomias fissibarbis; Melanostomias valdiviae; Bathophilus brevis; Pachystomias microdon; Bathophilus digitatus; Stomias boa; Eustomias bituberatus; Leptostomias macropogon; Neonesthes capensis; Leptostomias bilobatus; Chauliodus danae; Photonectes margarita; Leptostomias haplocaulus; Eustomias filifer; Photonectes leucospilus; Leptostomias gladiator; Photonectes caerulescens; Eustomias lipochirus; Astronesthes macropogon.*

CARB – Caribbean Province

Table G.3.1 Basic data (CARB) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
28	808	2016	13102.8	3928	102	21

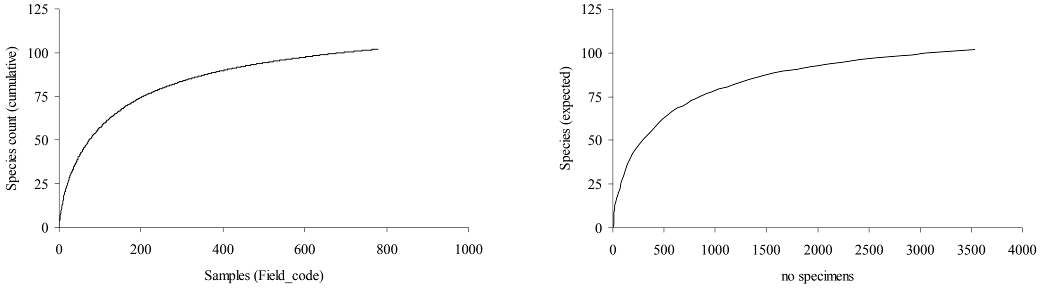


Figure G.3.1 Saturation curves (CARB); a) species samples plot; b) rarefaction.

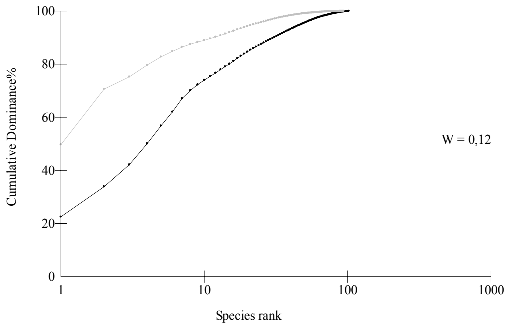


Figure G.3.2 Abundance-Biomass Curve (CARB). Grey: biomass; black: abundance.

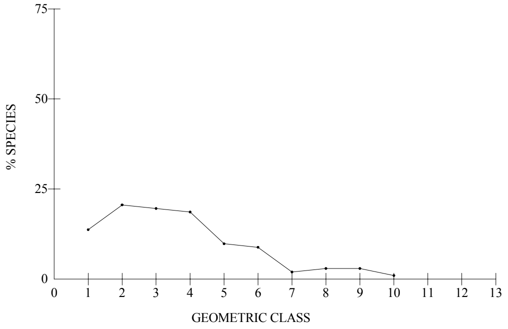


Figure G.3.3 Geometric plot (CARB).

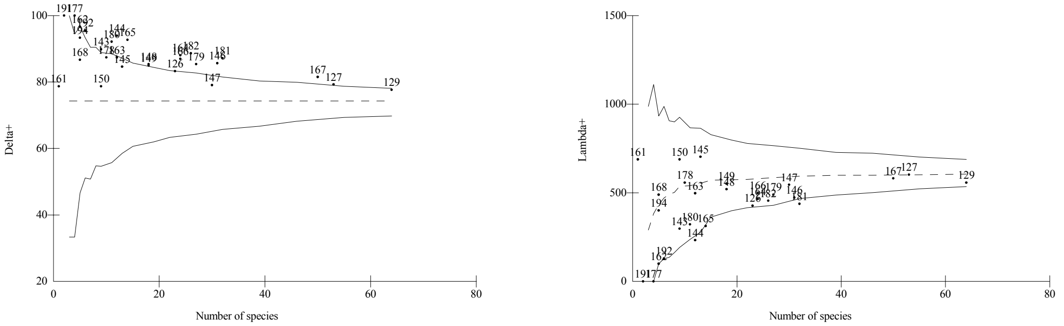


Figure G.3.4 Taxonomic funnels (CARB); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represents *sq_5x5* identification.

Table G.3.2 Regional and averaged local (grey) biodiversity indices (CARB) (see methods for details and indices acronyms).

	S	**d**	**H’**	**J’**	**1-λ’**	**N1**	**N2**	**N∞**	**Δ+**	**Λ+**	**Φ+**
Regional	102	30.65	3.13	0.68	0.95	22.85	11.12	4.44	74.3	609.2	42.2
mean	19.21	5.93	2.07	0.79	0.83	9.00	5.97	3.26	87.8	453.2	69.4
-95.0%	13.04	4.14	1.83	0.75	0.78	6.96	4.66	2.61	85.4	390.6	62.9
95.0%	25.39	7.71	2.31	0.84	0.88	11.05	7.28	3.92	90.3	515.8	75.8
min	1.00	0.26	0.64	0.55	0.45	1.00	1.00	1.00	77.6	100.0	45.3
max	64.00	18.17	3.02	0.97	1.02	20.44	16.09	9.11	100.0	703.5	100.0
n	28	27	27	27	27	28	28	28	27	25	28

Table G.3.3 Typical stomiid species assemblage (CARB); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus sloani	Widespread (anti-central)	28.4	9.5	1.4	30.5	30.5
Astronesthes macropogon	Amphi-Atlantic (distant neritic)	2.8	2.4	0.7	7.7	38.2
Stomias affinis	Amphi-Atlantic (distant neritic)	10.4	2.3	0.7	7.4	45.5
Photostomias guernei	Uncertain pattern	14.4	1.9	0.7	6.1	51.6
Idiacanthus fasciola	Tropical - Subtropical	6.4	1.8	0.6	5.8	57.4
Bathophilus pawneei	Caribbean complex	6.6	1.8	0.6	5.7	63.1
Astronesthes similis	Caribbean complex	3.8	1.2	0.5	3.8	66.9
Malacosteus niger	Widespread (anti-central)	1.3	1.1	0.5	3.5	70.4
Chauliodus danae	Tropical - Subtropical	8.5	1.0	0.4	3.1	73.4
Echiostoma barbatum	Caribbean complex	10.0	0.7	0.4	2.1	75.5
Eustomias brevibarbatus	Equatorial	1.2	0.6	0.4	2.1	77.6
Astronesthes niger	Uncertain pattern	2.1	0.6	0.4	2.1	79.6
Aristostomias xenostoma	Equatorial	1.6	0.6	0.4	2.0	81.7
Astronesthes richardsoni	Equatorial	1.0	0.6	0.4	2.0	83.6
Heterophotus ophistoma	Equatorial	0.4	0.5	0.3	1.5	85.1
Astronesthes atlanticus	Equatorial	1.6	0.4	0.3	1.3	86.4
Astronesthes micropogon	Amphi-Atlantic (distant neritic)	1.3	0.4	0.3	1.3	87.6
Eustomias enbarbatus	Equatorial complex	0.5	0.3	0.3	1.0	88.6
Bathophilus digitatus	Amphi-Atlantic (distant neritic)	1.0	0.3	0.3	0.9	89.5
Melanostomias melanops	Equatorial complex	0.7	0.3	0.3	0.8	90.3

Other species: *Eustomias variabilis; Melanostomias macrophotus; Stomias longibarbatus; Photonectes margarita; Eustomias fissibarbis; Eustomias polyaster; Flagellostomias boureei; Eustomias macrophthalmus; Eustomias bimargaritatus; Aristostomias polydactylus; Eustomias schmidti; Aristostomias lunifer; Eustomias bigelowi; Eustomias micraster; Eustomias macrurus; Aristostomias grimaldii; Melanostomias tentaculatus; Melanostomias biseriatus; Eustomias obscurus; Photonectes achirus; Melanostomias valdiviae; Bathophilus longipinnis; Eustomias longibarba; Bathophilus vaillanti; Borostomias mononema; Eustomias monoclonus; Bathophilus nigerrimus; Melanostomias margaritifer; Aristostomias tittmani; Photonectes caerulescens; Eustomias bituberatus; Photonectes mirabilis; Borostomias elucens; Eustomias paucifilis; Melanostomias melanopogon; Eustomias bibulbosus; Leptostomias bermudensis; Astronesthes gemmifer; Eustomias binghami; Leptostomias gladiator; Photonectes leucospilus; Eustomias xenobolus; Leptostomias bilobatus; Thysanactis dentex; Eustomias hypopsilus; Grammatostomias flagellibarba; Grammatostomias circularis; Eustomias dubius; Eustomias filifer; Eustomias melanostigma; Eustomias simplex; Eustomias triramis; Chirostomias pliopterus; Photonectes phyllopogon; Eustomias leptobolus; Eustomias arborifer; Pachystomias microdon; Melanostomias bartonbeani; Photonectes parvimanus; Leptostomias leptobolus*

CNRY – Eastern (Canary) Coastal Province

Table G.4.1 Basic data (CNRY) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
4	80	209	1393.1	772	36	17

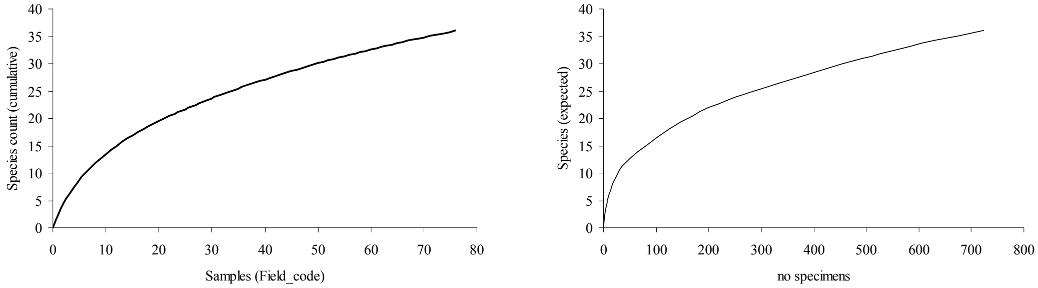


Figure G.4.1 Saturation curves (CNRY); a) species samples plot; b) rarefaction.

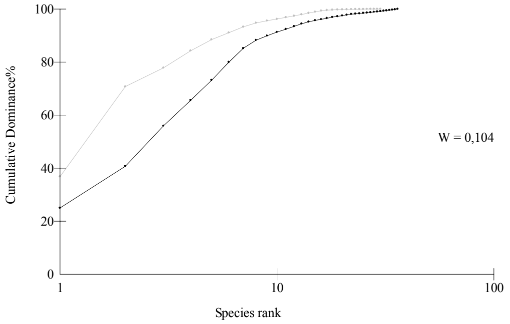


Figure G.4.2 Abundance-Biomass Curve (CNRY). Grey: biomass; black: abundance.

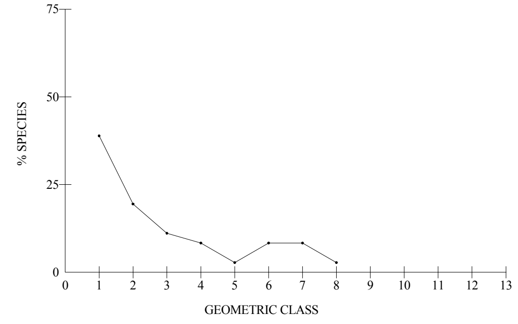


Figure G.4.3 Geometric plot (CNRY).

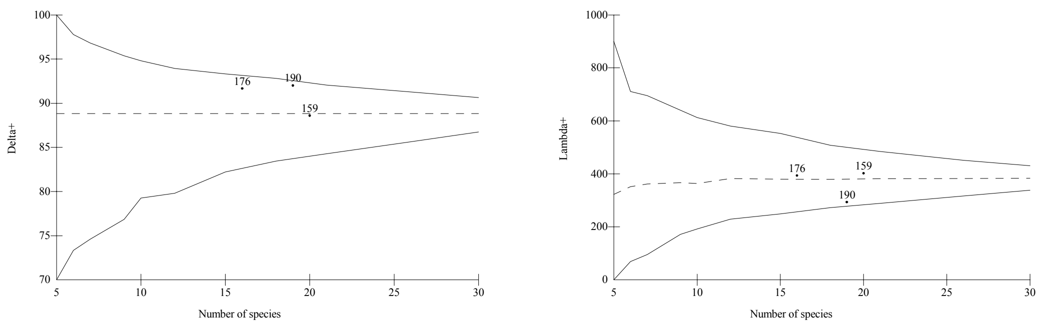


Figure G.4.4 Taxonomic funnels (CNRY); a) average taxonomic distinctness (Δ^{+}); b) variation in taxonomic distinctness (Λ^{+}); numbers represents *sq_5x5* identification.

Table G.4.2 Regional and averaged local (grey) biodiversity indices (CNRY) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	36	8.86	2.38	0.67	0.88	10.85	7.42	4.00	88.8	385.1	54.6
mean	18.33	4.49	1.91	0.66	0.78	6.95	4.72	2.91	90.8	363.0	63.6
-95.0%	13.16	2.70	1.19	0.47	0.48	2.34	0.27	0.12	86.1	213.0	60.5
95.0%	23.50	6.28	2.64	0.84	1.07	11.55	9.17	5.70	95.4	513.0	66.6
min	16.00	3.95	1.58	0.57	0.64	4.85	2.67	1.69	88.6	293.5	62.5
max	20.00	5.31	2.13	0.71	0.84	8.38	5.97	3.90	92.0	402.1	64.9
n	3	3	3	3	3	3	3	3	3	3	3

Table G.4.3 Typical stomiid species assemblage (CNRY); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus schmidti	Eastern Tropical - Equatorial	60.3	8.9	10.4	19.5	19.5
Chauliodus sloani	Widespread (anti-central)	36.7	7.5	27.0	16.5	36.0
Stomias boa boa	Mediterranean - Eastern Tropical	12.7	5.9	25.5	13.0	48.9
Stomias lampropeltis	Eastern Tropical - Equatorial	38.0	5.0	2.5	10.9	59.9
Flagellostomias boureei	Subtropical complex	3.3	4.3	4.1	9.5	69.3
Photostomias guernei	Uncertain pattern	1.3	3.8	17.0	8.3	77.6
Malacosteus niger	Widespread (anti-central)	16.3	2.2	0.6	4.8	82.5
Stomias affinis	Amphi-Atlantic (distant neritic)	7.3	1.7	0.6	3.8	86.2
Chauliodus danae	Tropical - Subtropical	18.3	1.6	0.6	3.5	89.7

Other species: *Odontostomias micropogon; Melanostomias biseriatus; Eustomias obscurus; Aristostomias polydactylus; Idiacanthus fasciola; Borostomias elucens; Astronesthes caulophorus; Bathophilus digitatus; Pachystomias microdon; Leptostomias haplocaulus; Bathophilus nigerrimus; Bathophilus vaillanti; Astronesthes richardsoni; Photonectes margarita; Stomias longibarbatus; Melanostomias bartonbeani; Melanostomias margaritifer; Melanostomias tentaculatus; Neonesthes capensis; OdontoStomias masticopogon; Photonectes braueri; Bathophilus brevis; Bathophilus longipinnis; Bathophilus pawneei; Borostomias mononema; Astronesthes macropogon; Astronesthes niger.*

NATR E – North Atlantic Tropical Gyral (East) Province

Table G.5.1 Basic data (NATR E) (see methods for explanations).

s_5x5 (n+)	*Field_code* (n)	*rec* (n)	Effort	spec (n)	sp (n)	Gen (n)
6+5	151	656	3733.2	2182	80	20

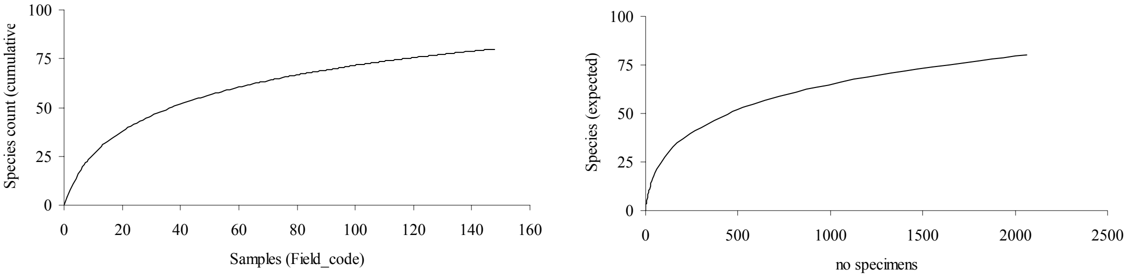


Figure G.5.1 Saturation curves (NATR E); a) species samples plot; b) rarefaction.

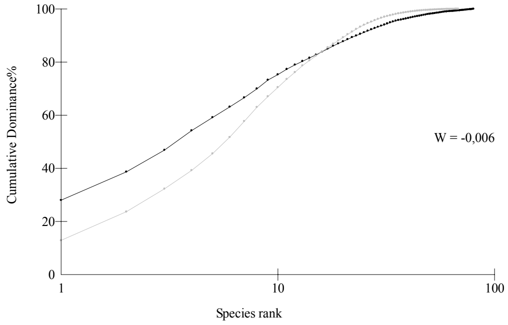


Figure G.5.2 Abundance-Biomass Curve (NATR E). Grey: biomass; black: abundance

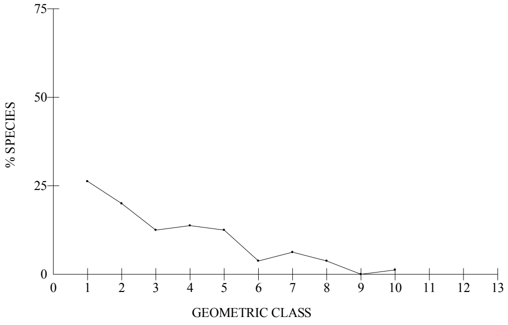


Figure G.5.3 Geometric plot (NATR E).

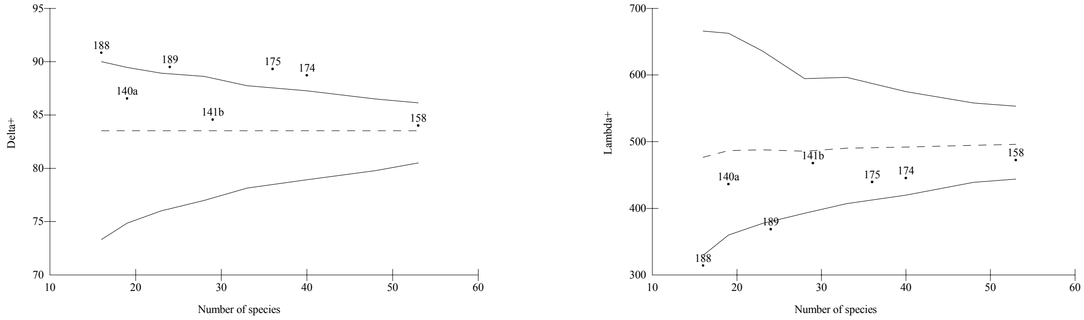


Figure G.5.4 Taxonomic funnels (NATR E); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.5.2 Regional and averaged local (grey) biodiversity indices (NATR E) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	80	19.69	2.94	0.67	0.90	18.93	8.93	3.57	83.5	496.4	44.2
mean	25.57	6.33	2.41	0.77	0.86	11.51	7.14	3.61	88.4	426.8	58.8
-95.0%	16.42	4.14	2.15	0.67	0.80	8.50	4.71	2.41	86.6	367.1	52.7
95.0%	34.72	8.52	2.67	0.86	0.93	14.53	9.58	4.81	90.3	486.6	64.9
min	14.00	2.76	2.02	0.63	0.78	7.57	4.28	2.24	84.6	314.1	51.7
max	40.00	8.81	2.80	0.88	0.97	16.44	10.89	6.00	90.8	507.2	68.8
n	7	7	7	7	7	7	7	7	7	7	7

Table G.5.3 Typical stomiid species assemblage (NATR E); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. Ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Photostomias guernei	Uncertain pattern	6.9	4.6	5.3	11.5	11.5
Eustomias obscurus	Subtropical complex	7.0	4.0	2.7	10.2	21.7
Astronesthes niger	Uncertain pattern	30.4	3.7	3.2	9.3	31.0
Melanostomias bartonbeani	Subtropical complex	3.3	2.5	1.5	6.2	37.1
Chauliodus danae	Tropical - Subtropical	15.4	2.4	0.8	6.0	43.2
Chauliodus sloani	Widespread (anti-central)	10.4	2.1	0.9	5.3	48.5
Idiacanthus fasciola	Tropical - Subtropical	20.0	2.1	0.8	5.2	53.7
Astronesthes atlanticus	Equatorial	4.6	1.8	0.9	4.6	58.3
Astronesthes micropogon	Amphi-Atlantic (distant neritic)	2.6	1.6	0.9	3.9	62.2
Flagellostomias boureei	Subtropical complex	2.0	1.4	0.9	3.6	65.8
Astronesthes richardsoni	Equatorial	9.6	1.4	0.6	3.5	69.3
Stomias affinis	Amphi-Atlantic (distant neritic)	21.7	1.1	0.6	2.9	72.2
Chauliodus schmidti	Eastern Tropical - Equatorial	13.7	1.1	0.6	2.8	75.0
Aristostomias xenostoma	Equatorial	2.4	0.9	0.6	2.4	77.4
Malacosteus niger	Widespread (anti-central)	2.4	0.9	0.6	2.2	79.6
Astronesthes gemmifer	Subtropical complex	1.1	0.7	0.6	1.7	81.3
Stomias brevibarbatus	Subtropical complex	1.6	0.7	0.6	1.7	83.0
Aristostomias polydactylus	Amphi-Atlantic (distant neritic)	0.6	0.7	0.6	1.7	84.7
Leptostomias gladiator	Subtropical complex	0.6	0.5	0.4	1.4	86.1
Photonectes margarita	Subtropical complex	1.4	0.5	0.4	1.2	87.2
Stomias lampropeltis	Eastern Tropical - Equatorial	5.7	0.4	0.4	1.1	88.4
Astronesthes macropogon	Amphi-Atlantic (distant neritic)	3.1	0.4	0.4	1.1	89.5
Melanostomias biseriatus	Subtropical complex	1.4	0.4	0.4	1.0	90.5

Other species: *Stomias longibarbatus; Photonectes mirabilis; Astronesthes caulophorus; Stomias boa boa; Eustomias filifer; Melanostomias tentaculatus; Photonectes leucospilus; Eustomias enbarbatus; Bathophilus nigerrimus; Photonectes dinema; Chirostomias pliopterus; Neonesthes capensis; Echiostoma barbatum; Leptostomias haplocaulus; Borostomias elucens; Bathophilus vaillanti; Leptostomias gracilis; Eustomias lipochirus; Leptostomias bilobatus; Eustomias schmidti; Eustomias melanostigma; Bathophilus digitatus; Astronesthes leucopogon.*

NATR – North Atlantic Tropical Gyral Province

Table G.6.1 Basic data (NATR) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
14+1	106	260	1234.7	523	60	19

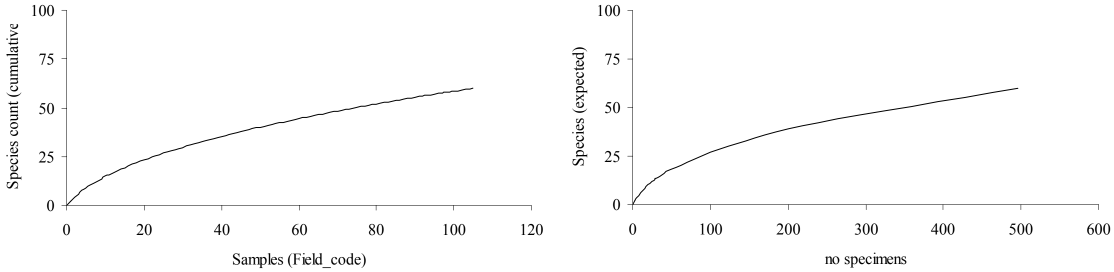


Figure G.6.1 Saturation curves (NATR); a) species samples plot; b) rarefaction.

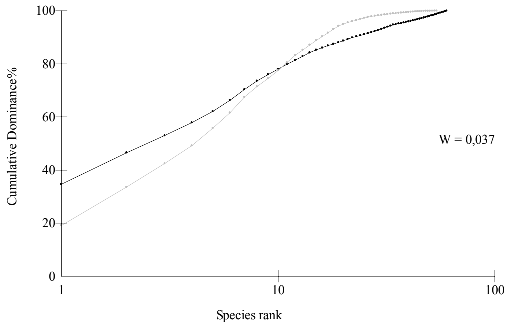


Figure G.6.2 Abundance-Biomass Curve (NATR). Grey: biomass; black: abundance.

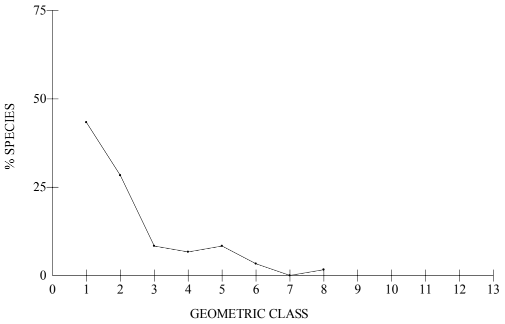


Figure G.6.3 Geometric plot (NATR).

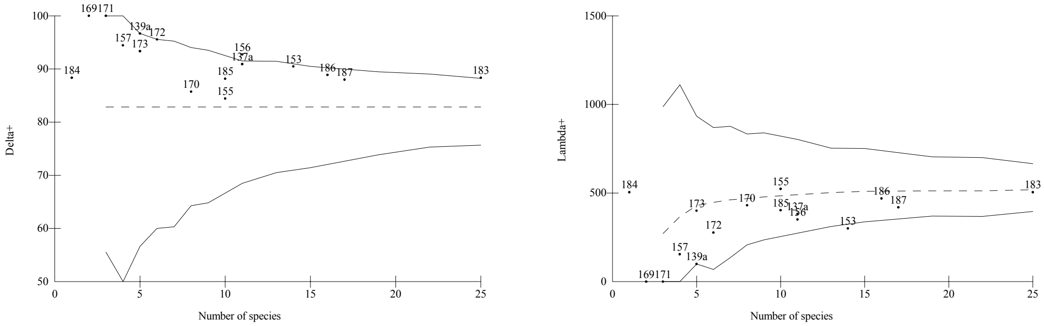


Figure G.6.4 Taxonomic funnels (NATR); a) average taxonomic distinctness (Δ^{+}); b) variation in taxonomic distinctness (Λ^{+}); numbers represent *sq_5x5* identification.

Table G.6.2 Regional and averaged local (grey) biodiversity indices (NATR) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	60	15.98	2.75	0.67	0.87	15.66	6.67	2.88	83.5	530.1	47.2
mean	11.61	3.12	1.59	0.73	0.67	6.17	4.27	2.52	91.1	375.7	77.8
-95.0%	5.77	1.32	1.20	0.62	0.56	3.61	2.63	1.85	88.6	308.0	70.2
95.0%	17.45	4.92	1.98	0.84	0.79	8.73	5.91	3.19	93.7	443.4	85.5
min	1.00	0.37	0.41	0.19	0.15	1.00	1.00	1.00	84.3	100.0	47.4
max	52.00	14.75	2.86	1.00	0.96	17.55	11.33	5.33	100.0	523.5	100.0
n	18	17	17	17	17	18	18	18	17	15	18

Table G.6.3 Typical stomiid species assemblage (NATR); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus danae	Tropical - Subtropical	35.7	7.3	0.8	29.4	29.4
Idiacanthus fasciola	Tropical - Subtropical	3.4	5.2	0.8	21.0	50.4
Photostomias guernei	Uncertain pattern	2.4	3.8	0.9	15.1	65.6
Chauliodus sloani	Widespread (anti-central)	1.8	1.7	0.5	6.8	72.4
Eustomias obscurus	Subtropical complex	2.3	1.5	0.5	5.9	78.2
Astronesthes niger	Uncertain pattern	3.7	1.0	0.3	4.1	82.3
Bathophilus pawneei	Caribbean complex	0.6	0.9	0.3	3.7	86.1
Astronesthes similis	Caribbean complex	0.6	0.7	0.3	2.6	88.7
Eustomias enbarbatus	Equatorial complex	0.6	0.3	0.3	1.3	90.0

Other species: *Astronesthes richardsoni; Bathophilus vaillanti; Astronesthes atlanticus; Melanostomias tentaculatus; Melanostomias melanopogon; Astronesthes leucopogon; Stomias affinis; Aristostomias xenostoma; Stomias longibarbatus; Thysanactis dentex; Heterophotus ophistoma; Stomias brevibarbatus; Bathophilus longipinnis; Bathophilus nigerrimus; Aristostomias polydactylus; Eustomias schmidti; Eustomias bigelowi; Photonectes caerulescens; Photonectes braueri; Melanostomias bartonbeani; Chauliodus schmidti; Flagellostomias boureei; Photonectes parvimanus; Malacosteus niger; Astronesthes micropogon; Melanostomias biseriatus; Leptostomias bilobatus; Bathophilus digitatus; Borostomias elucens; Melanostomias valdiviae; Eustomias lipochirus; Eustomias filifer; Leptostomias longibarba; Leptostomias gracilis; Astronesthes gemmifer; Eustomias melanostigma*

NATR (W) – North Atlantic Tropical Gyral (West) Province

Table G.7.1 Basic data (NATR W) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
2+14	285	769	8299.8	1859	74	18

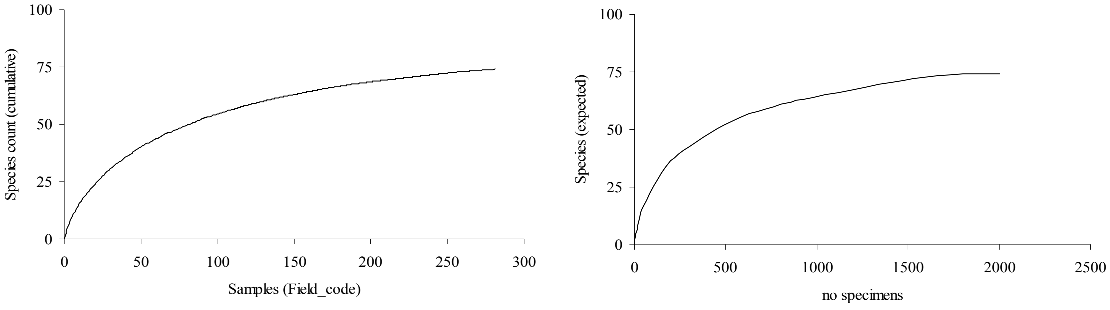


Figure G.7.1 Saturation curves (NATR W); a) species samples plot; b) rarefaction.

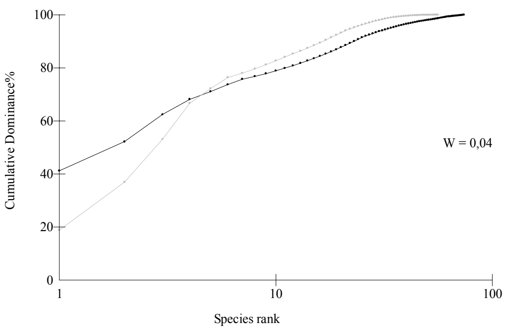


Figure G.7.2 Abundance-Biomass Curve (NATR W). Grey: biomass; black: abundance.

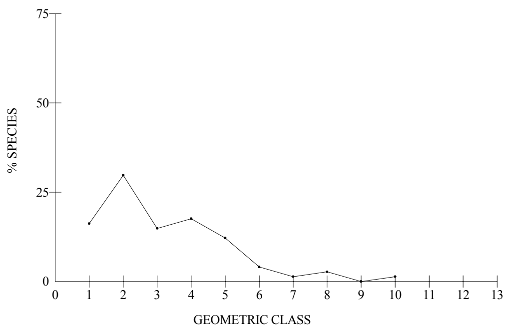


Figure G.7.3 Geometric plot (NATR W).

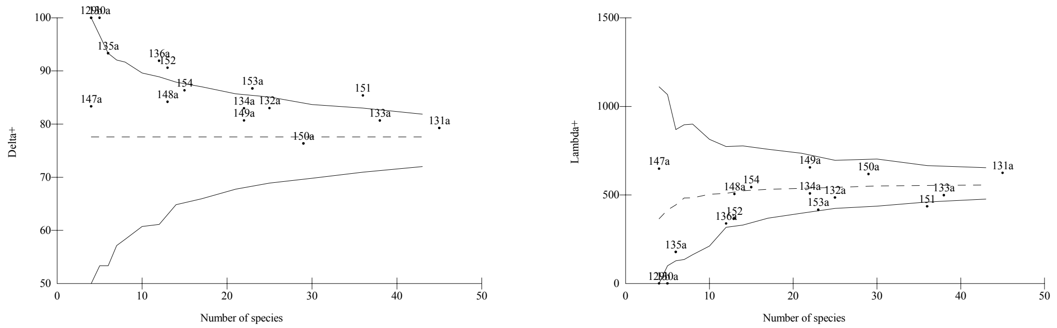


Figure G.7.4 Taxonomic funnels (NATR W), a) average taxonomic distinctness (Δ^{+}); b) variation in taxonomic distinctness (Λ^{+}); numbers represent *sq_5x5* identification.

Table G.7.2 Regional and averaged local (grey) biodiversity indices (NATR W) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	74	23.71	2.55	0.59	0.84	12.79	5.02	2.43	77.6	561.5	44.1
mean	19.50	6.11	1.88	0.72	0.79	7.59	4.49	2.51	86.5	487.3	68.3
-95.0%	12.70	3.95	1.60	0.64	0.71	5.21	3.19	1.99	82.8	409.8	59.7
95.0%	26.30	8.28	2.17	0.79	0.86	9.98	5.78	3.03	90.2	564.8	76.9
min	4.00	1.34	1.23	0.54	0.59	3.42	2.36	1.56	76.4	177.8	48.1
max	45.00	12.87	2.84	0.96	1.07	17.19	10.20	4.61	100.0	655.5	100.0
n	16	16	16	16	16	16	16	16	16	14	16

Table G.7.3 Typical stomiid species assemblage (NATR W); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus danae	Tropical - Subtropical	46.4	9.4	1.8	22.1	22.1
Idiacanthus fasciola	Tropical - Subtropical	12.4	5.3	1.4	12.4	34.5
Photostomias guernei	Uncertain pattern	11.6	5.0	1.3	11.7	46.2
Eustomias obscurus	Subtropical complex	6.4	4.2	1.4	9.9	56.1
Stomias brevibarbatus	Subtropical complex	2.9	4.1	1.2	9.7	65.8
Chauliodus sloani	Widespread (anti-central)	3.3	1.8	0.7	4.2	70.0
Eustomias binghami	Western Tropical Gyre	2.3	1.5	0.7	3.4	73.4
Echiostoma barbatum	Caribbean complex	1.2	1.2	0.5	2.8	76.2

Photonectes braueri	Western Tropical Gyre complex	1.0	1.2	0.6	2.7	78.9
Eustomias bimargaritatus	Western Tropical Gyre complex	1.2	1.0	0.6	2.2	81.1
Aristostomias lunifer	Western Tropical Gyre complex	1.1	0.7	0.5	1.7	82.9
Bathophilus pawneei	Caribbean complex	1.1	0.7	0.5	1.6	84.5
Eustomias enbarbatus	Equatorial complex	0.8	0.7	0.5	1.6	86.0
Melanostomias tentaculatus	Tropical - Equatorial	0.8	0.6	0.4	1.3	87.4
Neonesthes capensis	Subtropical complex	1.0	0.5	0.4	1.3	88.6
Photonectes parvimanus	Subtropical	0.8	0.5	0.4	1.2	89.8

Other species: *Eustomias fissibarbis; Eustomias macrophthalmus; Eustomias braueri; Astronesthes neopogon; Melanostomias valdiviae; Astronesthes niger; Melanostomias melanopogon; Stomias longibarbatus; Grammatostomias flagellibarba; Melanostomias margaritifer; Astronesthes atlanticus; Astronesthes similis; Eustomias bigelowi; Malacosteus niger; Eustomias simplex; Bathophilus vaillanti; Bathophilus longipinnis; Photonectes dinema; Eustomias tenisoni; Melanostomias biseriatus; Eustomias paucifilis; Grammatostomias circularis; Astronesthes macropogon; Bathophilus schizochirus; Grammatostomias dentatus; Eustomias hulleyi; Eustomias longibarba; Eustomias bituberatus; Heterophotus ophistoma; Astronesthes gemmifer; Chirostomias pliopterus; Aristostomias grimaldii; Melanostomias bartonbeani; Bathophilus nigerrimus; Leptostomias gladiator; Photonectes leucospilus; Leptostomias bilobatus; Aristostomias polydactylus; Eustomias lipochirus; Eustomias contiguus; Stomias affinis; Stomias boa; Astronesthes leucopogon; Eustomias radicifilis; Eustomias macrurus; Eustomias bibulbosus; Photonectes margarita; Photonectes mirabilis; Eustomias xenobolus; Flagellostomias boureei; Leptostomias haplocaulus; Leptostomias leptobolus; Eustomias micraster; Eustomias polyaster; Eustomias schmidti; Eustomias macronema; Eustomias brevibarbatus; Bathophilus digitatus.*

NAST W – North Atlantic Subtropical West Province

Table G.8.1 Basic data (NAST W) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
20+12	2257	5618	26809.2	11917	101	21

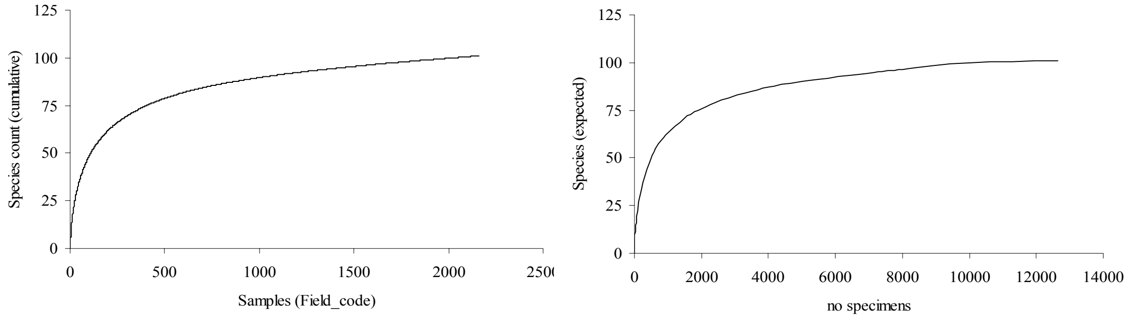


Figure G.8.1 Saturation curves (NAST W); a) species samples plot; b) rarefaction.

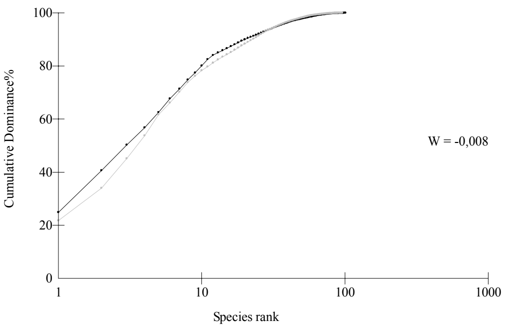


Figure G.8.2 Abundance-Biomass Curve (NAST W). Grey: biomass; black: abundance.

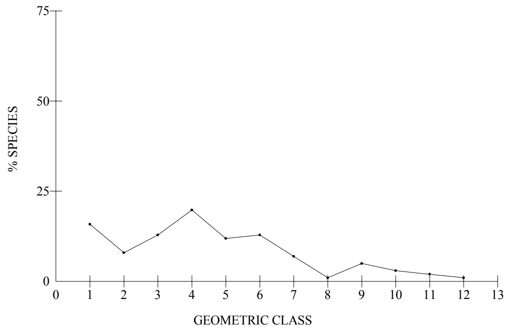


Figure G.8.3 Geometric plot (NAST W).

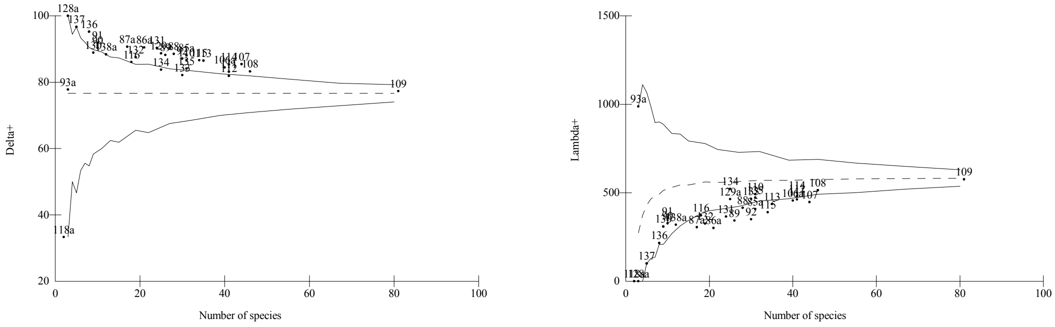


Figure G.8.4 Taxonomic funnels (NAST W); a) average taxonomic distinctness (Δ^{+}); b) variation in taxonomic distinctness (Λ^{+}); numbers represent *sq_5x5* identification.

Table G.8.2 Regional and averaged local (grey) biodiversity indices (NAST W) (see methods for details and indices acronyms).

	S	**d**	**H'**	**J'**	**1-λ'**	**N1**	**N2**	**N∞**	**Δ+**	**Λ+**	**Φ+**
Regional	101	27.02	2.85	0.62	0.91	17.35	8.95	4.02	76.7	583.1	42.2
mean	25.66	6.79	2.03	0.70	0.78	9.20	5.66	3.12	85.6	415.8	63.4
-95.0%	19.69	5.13	1.80	0.65	0.72	7.20	4.37	2.55	81.7	361.0	58.5
95.0%	31.62	8.46	2.27	0.75	0.83	11.20	6.95	3.69	89.4	470.6	68.3
min	2.00	0.32	0.63	0.39	0.28	1.88	1.39	1.19	33.3	100.0	43.6
max	81.00	22.05	3.21	1.00	1.00	24.66	17.71	8.09	100.0	987.7	100.0
n	32	32	32	32	32	32	32	32	32	30	32

Table G.8.3 Typical stomiid species assemblage (NAST W); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus danae	Tropical - Subtropical	84.4	6.7	1.6	15.4	15.4
Chauliodus sloani	Widespread (anti-central)	53.6	4.3	1.1	9.9	25.3
Idiacanthus fasciola	Tropical - Subtropical	19.6	3.7	1.5	8.6	33.9
Bathophilus vaillanti	Subtropical	12.4	3.7	1.3	8.6	42.5
Photostomias guernei	Uncertain pattern	32.7	3.0	1.3	7.0	49.5
Eustomias obscurus	Subtropical complex	8.9	2.6	1.2	5.9	55.4
Stomias boa ferox	Boreal complex	22.1	2.6	1.1	5.9	61.2
Astronesthes niger	Uncertain pattern	11.8	1.7	0.8	4.0	65.2
Malacosteus niger	Widespread (anti-central)	8.2	1.4	0.8	3.1	68.3
Echiostoma barbatum	Caribbean complex	5.3	1.2	0.7	2.8	71.2
Stomias brevibarbatus	Subtropical complex	9.0	1.2	0.7	2.7	73.9
Melanostomias bartonbeani	Subtropical complex	17.5	1.2	0.7	2.7	76.6
Chirostomias pliopterus	Subtropical complex	2.6	0.8	0.6	1.9	78.5
Photonectes margarita	Subtropical complex	3.3	0.8	0.5	1.7	80.2
Photonectes parvimanus	Subtropical	1.8	0.5	0.4	1.1	81.3
Astronesthes gemmifer	Subtropical complex	2.6	0.5	0.5	1.1	82.5
Photonectes dinema	Subtropical	2.4	0.5	0.5	1.1	83.5
Astronesthes leucopogon	Subtropical complex	2.3	0.5	0.5	1.0	84.6
Flagellostomias boureei	Subtropical complex	1.3	0.4	0.4	0.9	85.5
Melanostomias tentaculatus	Tropical - Equatorial	0.7	0.4	0.4	0.9	86.5
Photonectes braueri	Western Tropical Gyre complex	1.1	0.4	0.5	0.9	87.4
Aristostomias tittmanni	Subtropical complex	2.8	0.4	0.4	0.9	88.2
Stomias longibarbatus	Broadly Tropical	1.0	0.3	0.4	0.7	88.9
Melanostomias melanops	Equatorial complex	1.3	0.3	0.4	0.7	89.7
Melanostomias valdiviae	Western Tropical Gyre complex	0.8	0.3	0.4	0.7	90.3

Other species: *Eustomias filifer; Leptostomias gladiator; Astronesthes similis; Neonesthes capensis; Aristostomias lunifer; Bathophilus pawneei; Eustomias enbarbatus; Stomias affinis; Bathophilus longipinnis; Photonectes leucospilus; Bathophilus nigerrimus; Melanostomias melanopogon; Astronesthes macropogon; Melanostomias biseriatus; Pachystomias microdon; Astronesthes neopogon; Aristostomias polydactylus; Eustomias bibulbosus; Astronesthes micropogon; Eustomias schmidti; Aristostomias grimaldii; Bathophilus brevis; Eustomias braueri; Eustomias schiffi; Eustomias macrurus; Eustomias binghami; Trigonolampa miriceps; Eustomias contiguus; Eustomias parri; Eustomias lipochirus; Grammatostomias flagellibarba; Leptostomias haplocaulus; Aristostomias xenostoma; Eustomias fissibarbis; Eustomias longibarba; Eustomias bigelowi; Eustomias borealis; Eustomias bimargaritatus; Bathophilus digitatus; Astronesthes cyclophotus; Astronesthes richardsoni; Eustomias simplex; Leptostomias bermudensis; Eustomias satterleei; Photonectes mirabilis; Eustomias macronema; Grammatostomias dentatus; Eustomias monodactylus; Eustomias radicifilis; Grammatostomias circularis; Bathophilus altipinnis; Melanostomias margaritifer; Eustomias dubius; Leptostomias analis; Rhadinesthes decimus; Eustomias tetranema; Bathophilus proximus; Eustomias furcifer; Eustomias hulleyi.*

GFST – Gulf Stream Province

Table G.9.1 Basic data (GFST) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
11	1275	3384	29245.9	13253	83	23

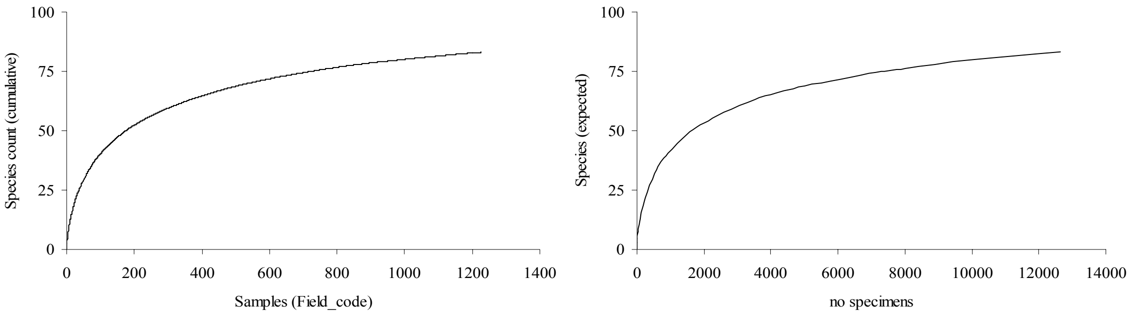


Figure G.9.1 Saturation curves (GFST); a) species samples plot; b) rarefaction.

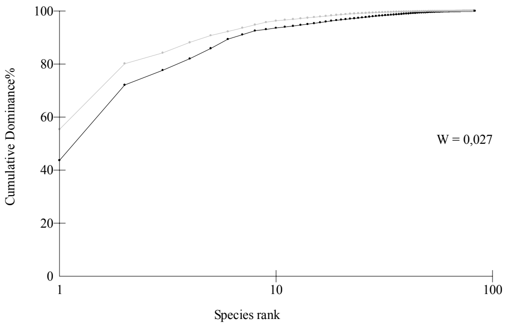


Figure G.9.2 Abundance-Biomass Curve (GFST). Grey: biomass; black: abundance.

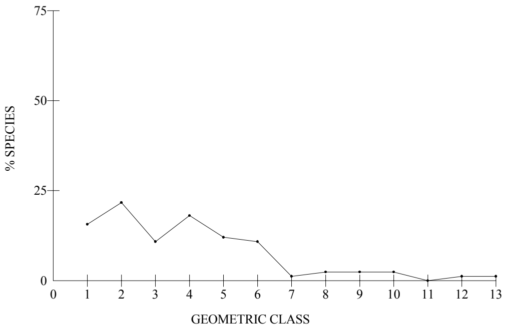


Figure G.9.3 Geometric plot (GFST).

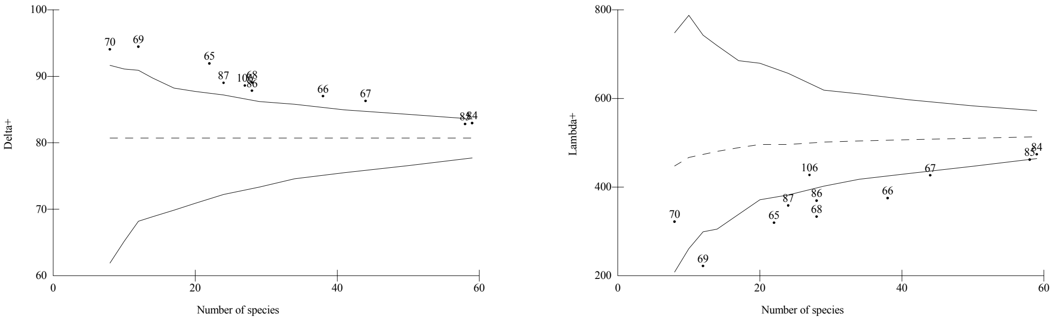


Figure G.9.4 Taxonomic funnels (GFST); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.9.2 Regional and averaged local (grey) biodiversity indices (GFST) (see methods for details and indices acronyms).

	S	**d**	**H'**	**J'**	**1-λ'**	**N1**	**N2**	**N∞**	**Δ+**	**Λ+**	**Φ+**
Regional	83	21.78	1.86	0.42	0.74	6.43	3.57	2.29	80.7	513.8	45.0
mean	31.64	8.79	1.82	0.55	0.75	7.19	4.38	2.61	88.5	371.6	59.9
-95.0%	20.43	5.78	1.43	0.45	0.64	4.50	2.84	1.95	86.0	322.2	52.9
95.0%	42.84	11.81	2.22	0.65	0.85	9.89	5.92	3.27	91.1	421.0	67.0
min	8.00	1.60	0.97	0.35	0.53	2.64	2.13	1.62	82.8	221.7	46.9
max	59.00	14.71	2.59	0.79	1.03	13.37	8.00	4.36	94.4	473.8	79.2
N	11	11	11	11	11	11	11	11	11	11	11

Table G.9.3 Typical stomiid species assemblage (GFST); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus sloani	Widespread (anti-central)	501.6	8.5	3.3	15.7	15.7
Stomias boa ferox	Boreal complex	326.1	6.5	1.8	12.0	27.8
Photostomias guernei	Uncertain pattern	49.8	4.0	4.4	7.4	35.1
Astronesthes niger	Uncertain pattern	64.0	3.9	2.8	7.3	42.4
Chauliodus danae	Tropical - Subtropical	44.6	3.8	3.9	7.1	49.5
Idiacanthus fasciola	Tropical - Subtropical	16.9	3.7	3.7	6.8	56.3
Melanostomias bartonbeani	Subtropical complex	39.7	3.1	1.9	5.8	62.1
Malacosteus niger	Widespread (anti-central)	19.7	2.4	1.2	4.5	66.5
Photonectes margarita	Subtropical complex	6.2	1.6	1.3	3.0	69.5
Bathophilus vaillanti	Subtropical	5.7	1.6	1.3	2.9	72.4
Echiostoma barbatum	Caribbean complex	4.1	1.4	1.2	2.6	75.0
Astronesthes similis	Caribbean complex	3.7	1.1	0.9	2.1	77.1
Stomias brevibarbatus	Subtropical complex	4.5	1.1	1.0	2.1	79.1
Aristostomias tittmanni	Subtropical complex	4.0	0.9	0.8	1.6	80.7
Chirostomias pliopterus	Subtropical complex	4.0	0.8	0.7	1.5	82.2
Aristostomias polydactylus	Amphi-Atlantic (distant neritic)	1.3	0.8	0.7	1.4	83.7
Astronesthes macropogon	Amphi-Atlantic (distant neritic)	2.6	0.7	0.6	1.2	84.9
Leptostomias gladiator	Subtropical complex	3.3	0.6	0.6	1.1	85.9
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	3.6	0.6	0.6	1.1	87.0
Astronesthes gemmifer	Subtropical complex	1.9	0.6	0.6	1.0	88.0
Flagellostomias boureei	Subtropical complex	1.9	0.5	0.6	0.9	88.9
Bathophilus pawneei	Caribbean complex	2.1	0.5	0.6	0.9	89.7
Eustomias schmidti	Caribbean complex	1.7	0.5	0.6	0.8	90.6

Other species: *Stomias affinis; Bathophilus longipinnis; Stomias longibarbatus; Melanostomias tentaculatus; Melanostomias biseriatus; Eustomias bibulbosus; Astronesthes leucopogon; Photonectes mirabilis; Eustomias obscurus; Melanostomias melanopogon; Pachystomias microdon; Bathophilus digitatus; Eustomias enbarbatus; Aristostomias grimaldii; Photonectes parvimanus; Astronesthes micropogon; Melanostomias valdiviae; Neonesthes capensis; Melanostomias melanops; Photonectes braueri; Aristostomias lunifer; Leptostomias haplocaulus; Eustomias filifer; Eustomias braueri; Grammatostomias flagellibarba; Eustomias borealis; Bathophilus brevis; Grammatostomias dentatus; Leptostomias bilobatus; Leptostomias longibarba; Photonectes leucospilus; Trigonolampa miriceps; Eustomias parri; Heterophotus ophistoma; Eustomias satterleei; Eustomias simplex; Eustomias schiffi; Bathophilus altipinnis; Eustomias bigelowi; Aristostomias xenostoma; Eustomias macrurus; Eustomias polyaster; Eustomias macronema; Eustomias dubius; Photonectes dinema; Grammatostomias circularis.*

NAST E– North Atlantic Subtropical East Province

Table G.10.1 Basic data (NAST E) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
16+9	782	2279	19146.6	7458	73	21

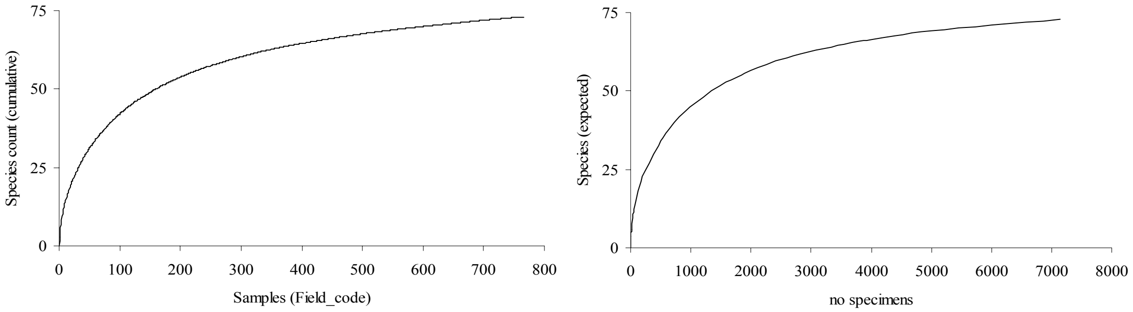


Figure G.10.1 Saturation curves (NAST E); a) species samples plot; b) rarefaction.

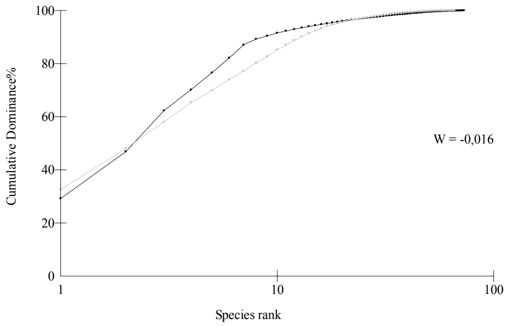


Figure G.10.2 Abundance-Biomass Curve (NAST E). Grey: biomass; black: abundance.

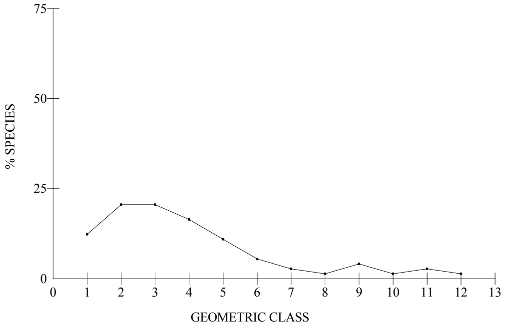


Figure G.10.3 Geometric plot (NAST E).

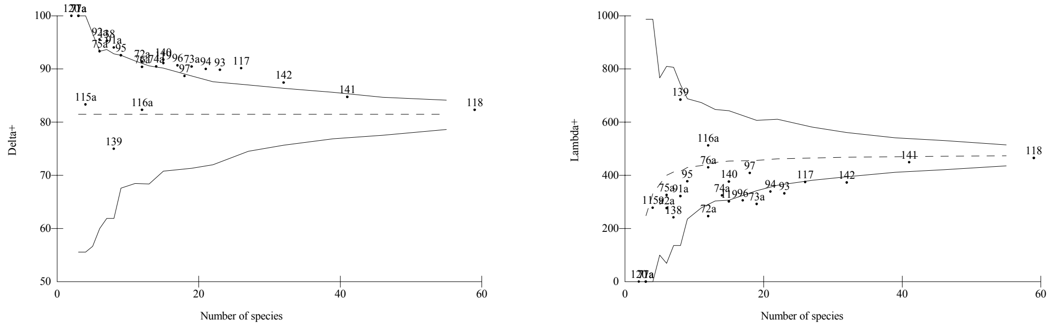


Figure G.10.4 Taxonomic funnels (NAST E); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.10.2 Regional and averaged local (grey) biodiversity indices (NAST E) (see methods for details and indices acronyms).

	S	**d**	**H'**	**J'**	**1-λ'**	**N1**	**N2**	**N∞**	**Δ+**	**Λ+**	**Φ+**
Regional	73	19.90	2.34	0.55	0.87	10.38	6.36	3.42	81.5	476.5	45.7
mean	15.68	4.18	1.53	0.64	0.67	5.17	3.42	2.21	90.4	365.3	73.2
-95.0%	10.28	2.68	1.31	0.58	0.60	4.15	2.78	1.83	88.0	320.8	67.3
95.0%	21.08	5.68	1.74	0.71	0.75	6.19	4.06	2.59	92.8	409.8	79.1
min	2.00	0.33	0.18	0.13	0.07	1.20	1.07	1.04	75.0	241.9	47.5
max	59.00	16.32	2.45	0.92	0.89	11.59	7.63	4.86	100.0	684.5	100.0
n	25	25	25	25	25	25	25	25	25	22	25

Table G.10.3 Typical stomiid species assemblage (NAST E); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Chauliodus sloani	Widespread (anti-central)	44.0	7.9	1.1	18.5	18.5
Chauliodus danae	Tropical - Subtropical	83.4	6.4	1.2	15.0	33.5
Stomias boa ferox / S. b. boa	Boreal complex / Mediterranean - Eastern Tropical	50.4	6.2	0.9	14.6	48.0
Bathophilus vaillanti	Subtropical	14.0	5.5	1.4	12.8	60.9
Idiacanthus fasciola	Tropical - Subtropical	18.2	3.7	1.0	8.7	69.6
Photostomias guernei	Uncertain pattern	22.4	3.0	0.8	7.1	76.6
Eustomias obscurus	Subtropical complex	15.9	2.7	0.8	6.3	82.9
Astronesthes niger	Uncertain pattern	6.4	1.4	0.5	3.3	86.2
Stomias brevibarbatus	Subtropical complex	3.2	0.7	0.5	1.6	87.8
Malacosteus niger	Widespread (anti-central)	3.4	0.7	0.4	1.6	89.4

Other species: *Astronesthes gemmifer; Melanostomias bartonbeani; Flagellostomias boureei; Aristostomias tittmani; Echiostoma barbatum; Chirostomias pliopterus; Bathophilus nigerrimus; Photonectes braueri; Stomias longibarbatus; Leptostomias haplocaulus; Eustomias filifer; Bathophilus longipinnis; Astronesthes leucopogon; Neonesthes capensis; Eustomias tetranema; Melanostomias valdiviae; Rhadinesthes decimus; Bathophilus digitatus; Eustomias macronema; Eustomias schmidti; Trigonolampa miriceps; Astronesthes atlanticus; Astronesthes neopogon; Melanostomias biseriatus; Melanostomias macrophotus; Eustomias braueri; Astronesthes micropogon; Photonectes margarita; Melanostomias melanops; Eustomias simplex; Photonectes parvimanus; Melanostomias tentaculatus; Astronesthes cyclophotus; Grammatostomias flagellibarba; Aristostomias grimaldii; Eustomias longibarba; Pachystomias microdon; Photonectes dinema; Eustomias lipochirus; Aristostomias xenostoma; Leptostomias longibarba; Photonectes mirabilis; Borostomias mononema; Photonectes leucospilus; Grammatostomias dentatus; Aristostomias lunifer*

NADR – North Atlantic Drift Province

Table G.11.1 Basic data (NADR) (see methods for explanations).

s_5x5 (n+)	*Field_code* (n)	*rec* (n)	Effort	spec (n)	sp (n)	Gen (n)
26	331	648	17627.2	4215	36	20

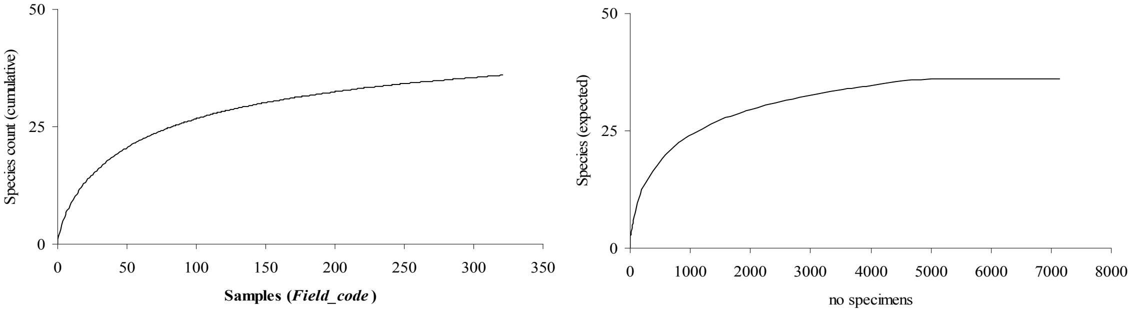


Figure G.11.1 Saturation curves (NADR); a) species samples plot; b) rarefaction.

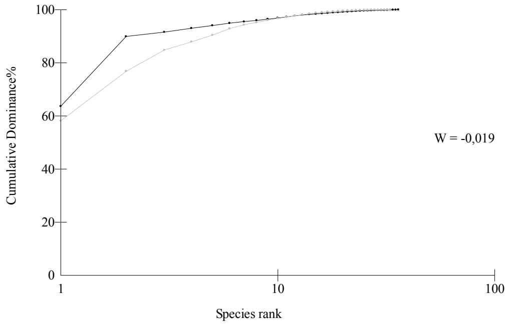


Figure G.11.2 Abundance-Biomass Curve (NADR). Grey: biomass; black: abundance.

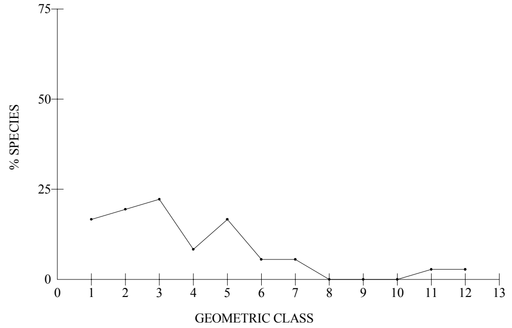


Figure G.11.3 Geometric plot (NADR).

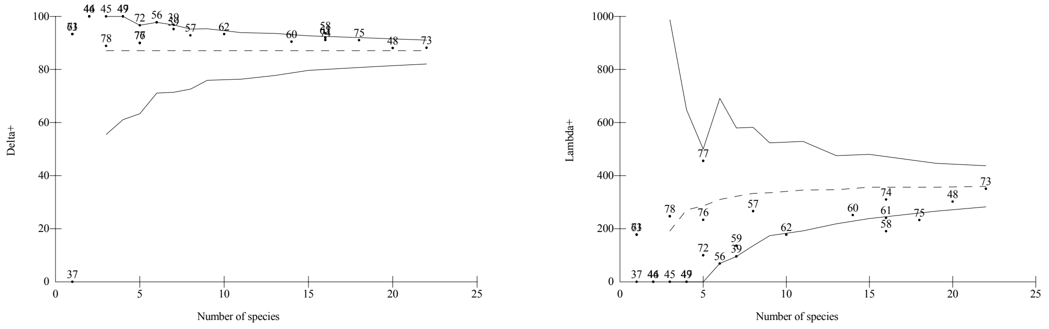


Figure G.11.4 Taxonomic funnels (NADR); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.11.2 Regional and averaged local (grey) biodiversity indices (NADR) (see methods for details and indices acronyms).

	S	d	H'	J'	1-λ'	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	36	11.07	1.16	0.32	0.55	3.19	2.11	1.57	87.1	366.0	57.4
mean	7.58	2.98	0.94	0.53	0.49	2.78	2.05	1.58	94.6	227.8	88.3
-95.0%	4.99	1.72	0.70	0.41	0.37	2.03	1.61	1.32	92.6	172.5	83.4
95.0%	10.16	4.25	1.19	0.64	0.62	3.53	2.48	1.83	96.6	283.1	93.1
min	1.00	0.22	0.21	0.10	0.09	1.00	1.00	1.00	88.1	69.1	63.6
max	22.00	11.41	1.93	0.99	0.92	6.89	4.41	3.00	100.0	455.6	100.0
n	26	23	23	23	23	26	26	26	23	16	26

Table G.11.3 Typical stomiid species assemblage (NADR); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. Ab**	**Av. S**	**S (sd)**	**C %**	**Cm %**
Stomias boa ferox	Boreal complex	101.7	27.2	1.6	57.7	57.7
Chauliodus sloani	Widespread (anti-central)	42.0	10.7	1.1	22.8	80.5
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	2.3	2.1	0.5	4.4	84.9
Melanostomias bartonbeani	Subtropical complex	2.7	1.6	0.5	3.3	88.2
Trigonolampa miriceps	Boreal	1.7	1.0	0.4	2.2	90.4

Other species: *Chirostomias pliopterus; Photostomias guernei; Astronesthes gemmifer; Malacosteus niger; Rhadinesthes decimus; Flagellostomias boureei; Astronesthes niger; Grammatostomias flagellibarba; Neonesthes capensis; Idiacanthus fasciola; Leptostomias haplocaulus; Leptostomias gladiator; Bathophilus nigerrimus; Pachystomias microdon; Photonectes margarita; Bathophilus vaillanti; Aristostomias tittmani; Leptostomias analis; Photonectes braueri; Chauliodus danae; Astronesthes leucopogon; Stomias longibarbatus; Photonectes caerulescens; Eustomias filifer; Stomias affinis; Leptostomias longibarba; Photonectes mirabilis; Melanostomias macrophotus; Melanostomias valdiviae; Photonectes achirus; Bathophilus longipinnis.*

NWCS – Northwest Atlantic Shelves Province

Table G.12.1 Basic data (NWCS) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
6+1	53	89	1111.1	942	15	12

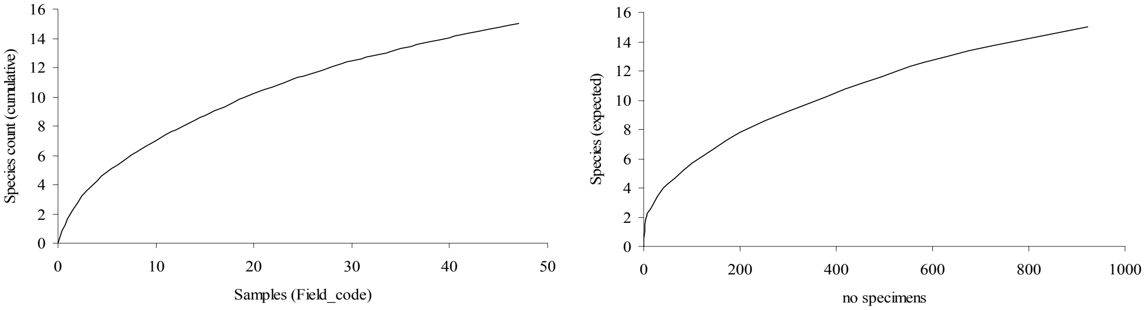


Figure G.12.1 Saturation curves (NWCS); a) species samples plot; b) rarefaction.

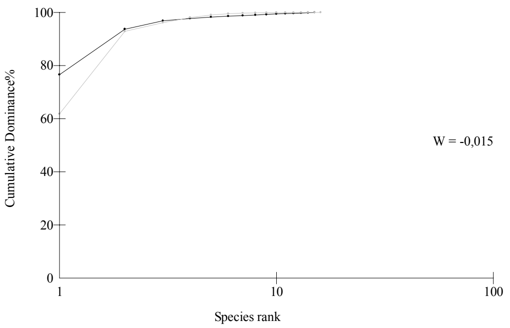


Figure G.12.2 Abundance-Biomass Curve (NWCS). Grey: biomass; black: abundance.

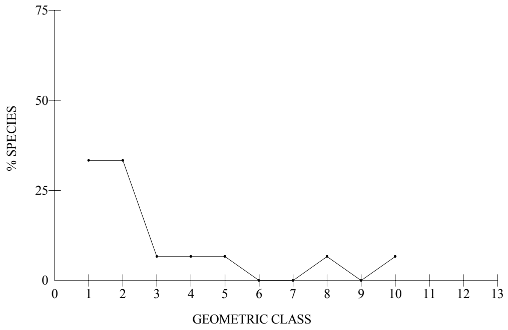


Figure G.12.3 Geometric plot (NWCS).

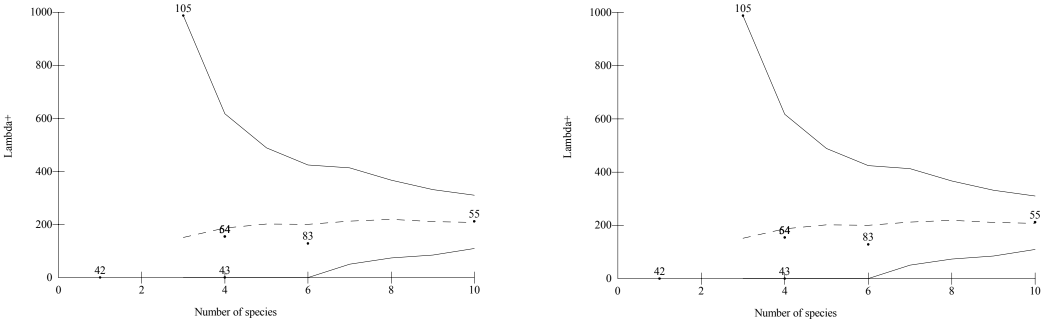


Figure G.12.4 Taxonomic funnels (NWCS); a) average taxonomic distinctness (Δ^+); b) variation in taxonomic distinctness (Λ^+); numbers represent *sq_5x5* identification.

Table G.12.2 Regional and averaged local (grey) biodiversity indices (NWCS) (see methods for details and indices acronyms).

	S	d	H'	J'	1-λ'	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	15	3.17	0.79	0.29	0.39	2.21	1.62	1.31	94.6	214.3	73.3
mean	4.43	1.33	1.06	0.74	0.62	2.83	2.64	2.43	92.7	327.3	90.0
-95.0%	1.77	0.40	0.60	0.43	0.35	1.36	1.12	0.96	84.7	-132.6	81.9
95.0%	7.09	2.25	1.52	1.06	0.89	4.31	4.16	3.89	100.7	787.2	98.1
min	1.00	0.65	0.63	0.27	0.31	1.00	1.00	1.00	77.8	128.4	77.8
max	10.00	2.88	1.75	1.00	0.99	5.74	5.56	5.00	100.0	987.7	100.0
n	7	6	6	6	6	7	7	7	6	5	7

Table G.12.3 Typical stomiid species assemblage (NWCS); SIMPER analysis (see methods for details).

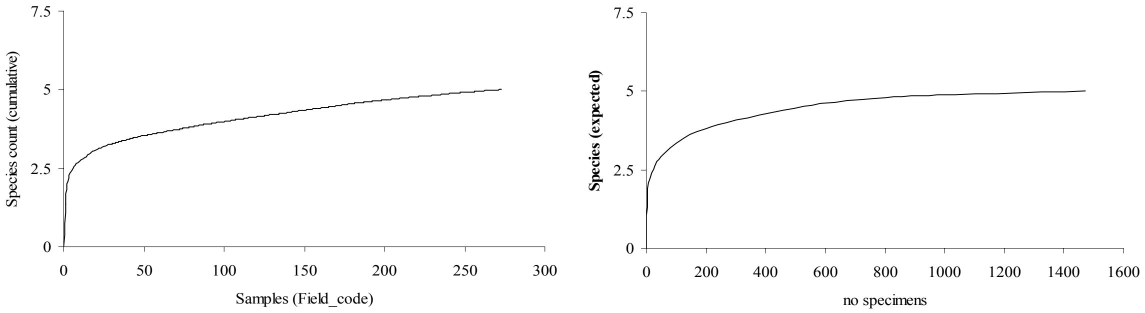
Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Stomias boa ferox	Boreal complex	100,9	7,3	0,6	33,4	33,4
Aristostomias tittmanni	Subtropical complex	0,7	4,2	0,5	19,3	52,7
Chauliodus sloani	Widespread (anti-central)	22,6	3,5	0,4	16,2	68,9
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	4,1	2,8	0,4	12,8	81,7
Melanostomias bartonbeani	Subtropical complex	1,1	1,9	0,4	8,8	90,6

Other species: *Chauliodus danae*; *Photostomias guernei*; *Photonectes margarita*; *Bathophilus vaillanti*.

MEDI – Mediterranean Sea Province

Table G.13.1 Basic data (MEDI) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
15	274	380	3434.5	1534	5	4



G.13.1 Saturation curves (MEDI); a) species samples plot; b) rarefaction.

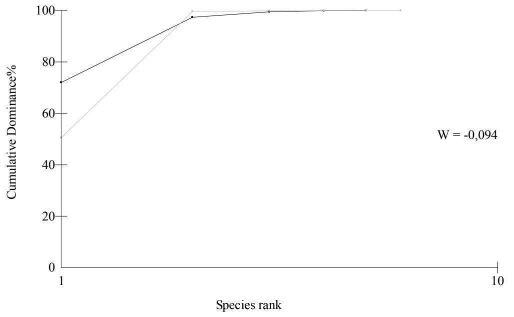


Figure G.13.2 Abundance-Biomass Curve (MEDI). Grey: biomass; black: abundance.

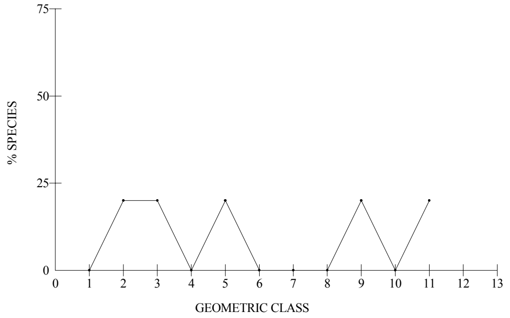


Figure G.13.3 Geometric plot (MEDI).

Table G.13.2 Regional and averaged local (grey) biodiversity indices (MEDI) (see methods for details and indices acronyms).

	S	**d**	**H'**	**J'**	**1-λ'**	**N1**	**N2**	**N∞**	**Δ+**	**Λ+**	**Φ+**
Regional	5	1.06	0.70	0.43	0.43	2.01	1.72	1.39	93.3	400.0	86.7
mean	2.47	0.56	0.68	0.66	0.37	1.74	1.60	1.41	98.0	987.7	98.5
-95.0%	1.88	0.40	0.54	0.50	0.24	1.43	1.33	1.20	93.5		95.3
95.0%	3.05	0.72	0.82	0.82	0.50	2.05	1.87	1.62	102.5		101.7
min	1.00	0.21	0.22	0.20	0.00	1.00	1.00	1.00	77.8		77.8
max	4.00	1.03	0.89	0.99	0.57	2.44	2.19	2.10	100.0		100.0
n	15	11	11	11	13	15	15	15	11	1	15

Table G.13.3 Typical stomiid species assemblage (MEDI); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Stomias boa boa	Mediterranean - Eastern Tropical	70.7	51.6	3.2	69.9	69.9
Chauliodus sloani	Widespread (anti-central)	24.9	17.4	1.0	23.6	93.5
Bathophilus nigerrimus	Mediterranean - Extended Eastern	2.1	4.7	0.6	6.4	99.8
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	0.1	0.1	0.1	0.2	100.0

(Stomias brevibarbatus just west of Gilbraltar)

SARC - Atlantic Subarctic Province

Table G.14.1 Basic data (SARC) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
5+3	43	68	2820.4	126	10	10

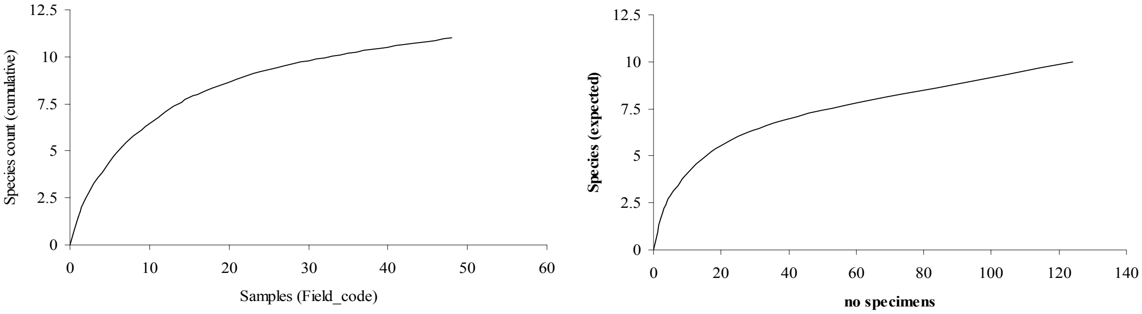


Figure G.14.1 Saturation curves (SARC); a) species samples plot; b) rarefaction.

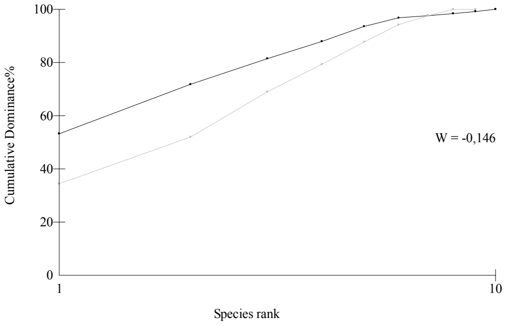


Figure G.14.2 Abundance-Biomass Curve (SARC). Grey: biomass; black: abundance.

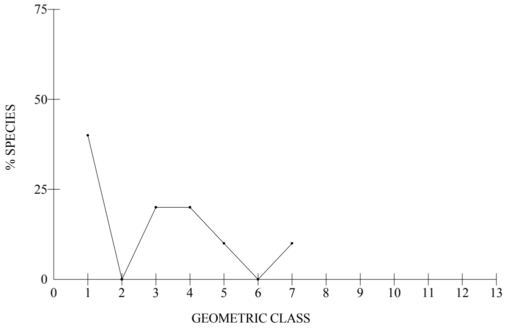


Figure G.14.3 Geometric plot (SARC).

Table G.14.2 Regional and averaged local (grey) biodiversity indices (SARC) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	10	6.08	1.48	0.64	0.86	4.39	2.98	1.88	91.9	205.2	83.3
mean	3.13	2.06	0.90	0.79	0.53	2.42	2.13	1.67	98.1	152.6	97.1
-95.0%	0.58	-0.87	0.26	0.56	0.14	0.86	0.93	0.99	94.6	515.8	92.0
95.0%	5.67	4.99	1.54	1.01	0.92	3.98	3.34	2.34	101.6	821.0	102.1
min	1.00	0.32	0.27	0.38	0.00	1.00	1.00	1.00	91.9	100.0	83.3
max	10.00	7.24	1.82	1.00	1.12	6.19	4.93	3.25	100.0	205.2	100.0
n	8	6	6	6	7	8	8	8	6	2	8

Table G.14.3 Typical stomiid species assemblage (SARC); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Stomias boa ferox	Boreal complex	8.3	48.3	2.2	84.7	84.7
Chauliodus sloani	Widespread (anti-central)	2.9	5.4	0.5	9.4	94.1
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	0.9	1.9	0.3	3.3	97.4
Trigonolampa miriceps	Boreal	1.5	0.6	0.2	1.0	98.4
Flagellostomias boureei	Subtropical complex	1.0	0.5	0.2	0.9	99.3
Melanostomias bartonbeani	Subtropical complex	0.5	0.4	0.2	0.7	100.0

ARCT–Atlantic Arctic Province

Table G.15.1 Basic data (ARCT) (see methods for explanations).

s_5x5 (n+)	***Field_code (n)***	***rec (n)***	***Effort***	***spec (n)***	***sp (n)***	***Gen (n)***
11	47	91	3810.8	240	8	8

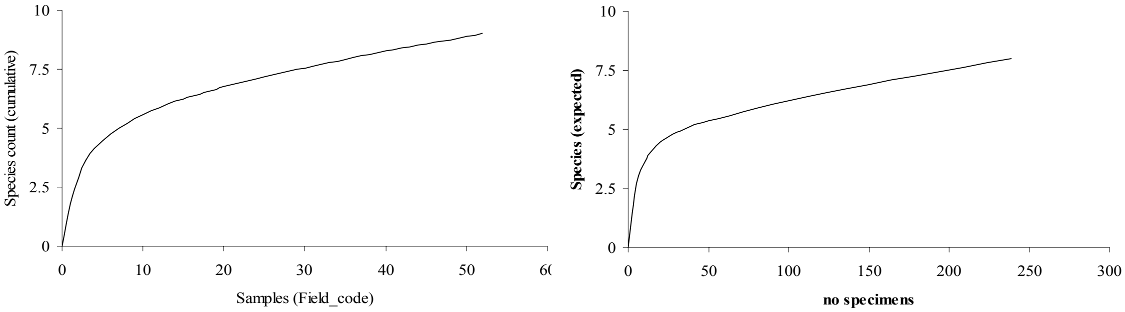


Figure G.15.1 Saturation curves (ARCT); a) species samples plot; b) rarefaction.

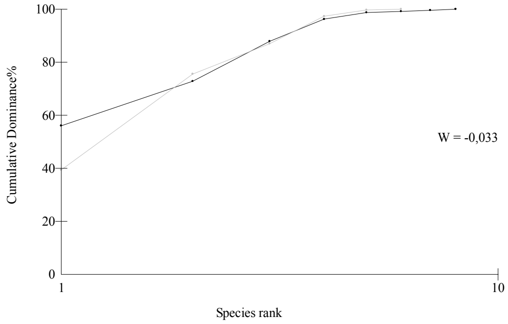


Figure G.15.2 Abundance-Biomass Curve (ARCT). Grey: biomass; black: abundance.

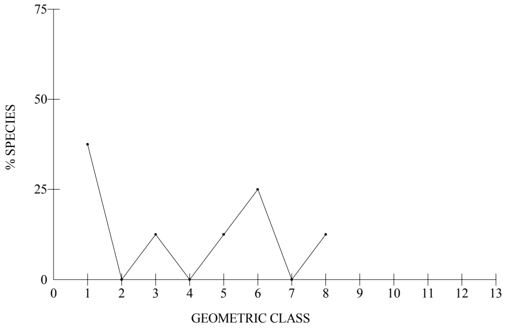


Figure G.15.3 Geometric plot (ARCT).

Table G.15.2 Regional and averaged local (grey) biodiversity indices (ARCT) (see methods for details and indices acronyms).

	S	d	H’	J’	1-λ’	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	8	3.81	1.28	0.61	0.75	3.59	2.68	1.78	95.2	136.1	87.5
mean	3.45	1.90	1.07	0.75	0.67	2.55	2.20	1.71	98.2	87.7	97.2
-95.0%	2.07	0.85	0.71	0.62	0.43	1.61	1.40	1.16	96.9	66.7	95.0
95.0%	4.84	2.95	1.43	0.87	0.90	3.50	3.00	2.25	99.5	108.6	99.4
min	1.00	0.29	0.38	0.53	0.23	1.00	1.00	1.00	96.7	69.1	93.3
max	6.00	3.68	1.51	0.94	1.02	4.53	4.27	3.54	100.0	100.0	100.0
n	11	8	8	8	8	11	11	11	8	5	11

Table G.15.3 Typical stomiid species assemblage (ARCT); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Stomias boa ferox	Boreal complex	12.2	30.9	1.4	55.0	55.0
Chauliodus sloani	Widespread (anti-central)	3.6	11.0	1.0	19.6	74.6
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	3.3	8.4	0.7	14.9	89.5
Malacosteus niger	Widespread (anti-central)	1.8	4.3	0.6	7.6	97.1
Rhadinesthes decimus	Extended Eastern	0.6	1.6	0.4	2.9	100.0

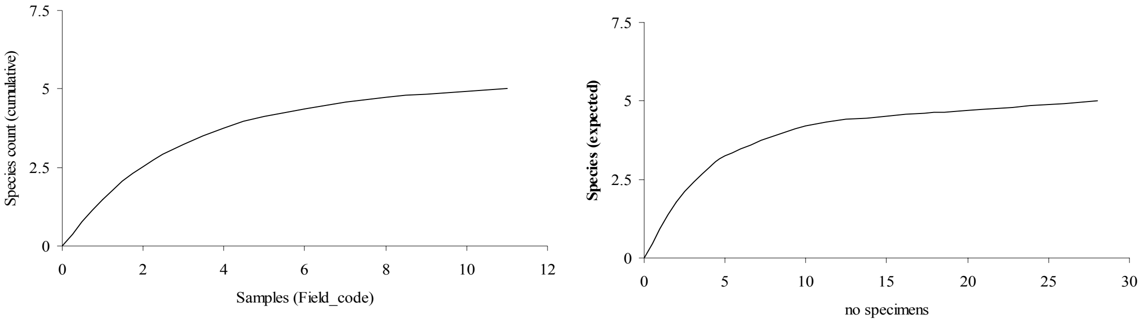
Other species: *Trigonolampa miriceps; Flagellostomias boureei*; *Melanostomias bartonbeani;*

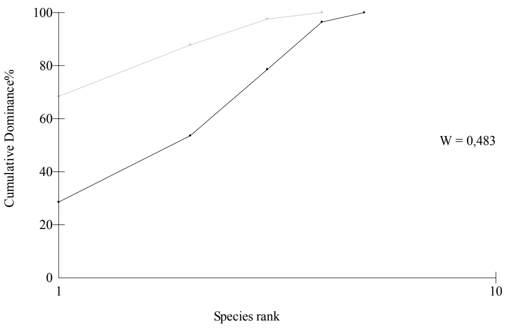
BPLR – Atlantic Boreal Polar Province

Table G.16.1 Basic data (BPLR) (see methods for explanations).

s_5x5 **(n+)**	***Field_code*** **(n)**	***rec*** **(n)**	**Effort**	**spec (n)**	**sp (n)**	**Gen (n)**
5	11	16	787.3	28	5	5

Figure G.16.1 Saturation curves (BPLR); a) species samples plot; b) rarefaction.





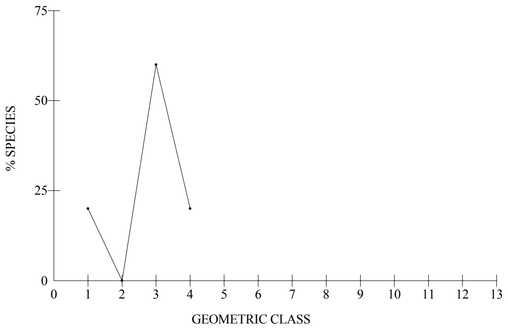


Figure G.16.2 Abundance-Biomass Curve (BPLR). Grey: biomass; black: abundance.

Figure G.16.3 Geometric plot (BPLR).

Table G.16.2 Regional and averaged local (grey) biodiversity indices (BPLR) (see methods for details and indices acronyms).

	S	d	H'	J'	1-λ'	N1	N2	N∞	Δ+	Λ+	Φ+
Regional	5	3.15	1.48	0.92	1.06	4.38	4.17	3.50	100.0		100.0
mean	2.40	2.18	0.94	0.97	1.13	2.35	2.30	2.13	100.0		100.0
-95.0%	0.98	0.13	0.40	0.91	0.45	0.98	0.98	0.97			
95.0%	3.82	4.24	1.48	1.03	1.82	3.71	3.63	3.30			
min	1.00	1.05	0.64	0.92	0.72	1.00	1.00	1.00	100.0		100.0
max	4.00	4.04	1.35	1.00	1.71	3.85	3.72	3.17	100.0		100.0
n	5	4	4	4	4	5	5	5	4	5	4

Table G.16.3 Typical stomiid species assemblage (BPLR); SIMPER analysis (see methods for details).

Species	**Biogeographic pattern**	**Av. ab**	**Av. Sm**	**Sm (sd)**	**C %**	**Cm %**
Borostomias antarcticus	Polar - Boreal / Mediterranean (west)	1,6	41,1	3,5	81,9	81,9
Malacosteus niger	Widespread (anti-central)	1,4	3,3	0,3	6,7	88,5
Stomias boa ferox	Boreal complex	1,4	3,0	0,3	5,9	94,4
Chauliodus sloani	Widespread (anti-central)	1,0	2,8	0,3	5,6	100,0