

Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species' sizes

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Received 22.4.1993

Accepted 10.1.1994

Key words: Fish reproductive style, Fish phylogeny, Vertical distribution, Pelagic, Demersal, Size spectra, Biomass spectra

Synopsis

The pelagic (589 spp.) and demersal (505 spp.) oceanic ichthyofaunas of the North Atlantic Basin have very different compositions at ordinal and family level. Yet the pattern of relationships between species' maximum size and maximum fecundity from data available (10% of the pelagic, 19% of the demersal species) was similar. A positive relationship between fecundity and weight was confirmed among most teleosts, but was not followed by the elasmobranchs represented. Species' reproductive styles are reviewed in ordinal groupings within a framework of the overall body size/fecundity distribution. Species size (maximum weight) spectra were synthesized for both pelagic and demersal assemblages to assess the allocation of potential reproductive effort throughout the North Atlantic oceanic ichthyofauna. The only available examples of species size spectra and biomass spectra from the pelagic and demersal ichthyofauna in this ocean basin imply geographic and bathymetric variation in overall reproductive effort among fishes whose fecundity is size dependent. Further implications concerning reproductive effort are discussed in the light of food availability.

Introduction

The first substantial review of reproduction among deep-sea fishes was published thirty years ago (Mead et al. 1964). Since then additions have been made at the species level (e.g. Kawaguchi & Marumo 1967, Badcock & Merrett 1976, Gjosaeter 1981, Fisher 1983, Nazarov 1983, Marshall 1984, Sulak et al. 1985, Wenner 1984, Crabtree et al. 1985, Oven 1985, Badcock 1986, Crabtree & Sulak 1986, Miya & Nemoto 1986a, b, 1987a, b, 1991, Mazhirina & Filin 1987, Pankhurst et al. 1987, Pankhurst 1988, Silverberg et al. 1987, Alekseyev et al. 1992) and family level (e.g. Nielsen et al. 1968, Nielsen 1969, Marshall 1973, Pietsch 1976, Stein 1980, Stein & Percy 1982, Kawaguchi & Mauchline 1987) and for broader

groupings (e.g. Marshall 1971, 1979, Gordon 1979a, b, Clarke 1983, 1984, Golovan & Pakhorukov 1984).

Mead et al. (1964) reviewed reproduction among oceanic fishes along phylogenetic lines. Almost 100 years ago Woodward (1898) wrote of the antiquity of the deep-sea fish fauna, declaring that 'those out-of-the-date forms of life which can no longer compete with the vigorous shore-dwelling races, are compelled to retreat to the freshwaters on the one hand, or to the deep-sea on the other'. Andriyashev (1953) expanded this view by recognizing groupings of ancient and secondary deep-water fishes. These works were general and only a few attempts have been made to approximate the total number of species and phylogenetic composition of the oceanic ichthyofauna overall (e.g. Cohen 1970, Parin 1984).

The aim of this study is to update the review of

Mead et al. (1964) and, through consideration of the ichthyofauna of a specific ocean basin, define patterns of reproductive styles and discuss underlying functionality. The basin considered is the North Atlantic, as part of an on-going study of the region and its ichthyofauna (Haedrich & Merrett 1988, 1992, Merrett et al. 1991a, b). Of necessity the results are preliminary, because detailed information on the reproduction of the majority of species represented still remains unknown. The most common parameters recorded are size [unfortunately, usually in terms of length; 'fish weights are almost never given' (Clarke 1984)] and fecundity. Since the size range of teleost eggs, at least pelagic ones, is not large in comparison with the size range of females (Ware 1975), fecundity can be used as a comparable index of reproductive effort.

The depth and associated gradients of the deep-sea (e.g. see Mann & Lazier 1991), especially the attenuation of sunlight, are major factors influencing oceanic life. A vast midwater realm, where food supply and predation pressure are relatively low, separates much thinner surface and benthic boundary layers where both these parameters are considerably higher. Depth influences the temperature structure strongly, resulting in the development of permanent and seasonal thermoclines. The structure of the seasonal thermocline has a substantial bearing upon the hatching time of embryos from pelagic eggs (Pauly & Pullin 1988), the evolution of which was the key to the efficient ichthyofaunal colonization of the deep-sea (Duarte & Alcaraz 1989). Balon (1984) pointed out that hatching time itself is of little survival value, but at higher temperature more rapid progress is made through vulnerable early larval stages.

Wootton (1992) used a theoretical approach to view the positions occupied by fish species in a multi-variate space whose dimensions were defined by life-history traits. He summarized a substantial array of life-history patterns. One of the several constraints on these that he considered was size. His remarks on body size, fecundity and egg size are all very relevant to the current work. He noted the substantial gap in egg volume between the minimum for oviparous elasmobranchs and the maximum for teleosts (by a factor of almost forty) and that each of

these extremes was rare. Yet he observed that elasmobranchs were able to produce ova well within the teleost size range but that these forms were viviparous and so the propagule released was still large.

Expanding on the fact that the egg mass produced by a female teleost at any one time is constrained by body size, Wootton (1992) reviewed the advantages gained by producing a large egg at the cost of a reduction in fecundity. He concluded that larger propagules should have a lower mortality rate, but that there was little or no advantage to pelagic spawners in producing larger eggs. Duarte & Alcaraz (1989) assessed the advantages of producing many small or few large eggs from among 51 species of mixed marine (mostly neritic) and freshwater fishes. They found no evidence of a phylogenetic trend towards greater egg sizes. In reworking the data used by Duarte & Alcaraz (1989), Elgar (1990) concluded, among other things, that the way in which reproductive output is partitioned between the size and number of offspring varies independently of body size. The general rule seems to be simply that pelagic spawning marine fish produce many small eggs (< 2 mm diameter, e.g. Duarte & Alcaraz 1989, Ware 1975) and demersal spawners produce fewer large eggs [but, in addition, Elgar (1990) pointed out that this trade-off can also be found across taxa]. Yet, if the efficient colonization of the oceanic environment did involve the evolution of pelagic eggs (Duarte & Alcaraz 1989), it follows that consideration must largely focus on the dependence on small eggs. Indeed, the data given by Crabtree & Sulak (1986) for deep demersal teleosts, at least, is consistent with this view. Hence the variation investigated is tacitly constrained within one of these two basic fecundity patterns.

Adams (1980) demonstrated that marine fish conform with the hypothetical r- and K- correlates in their life-history parameters. He showed that species on the r- end of the continuum inclined towards small body size, low maximum age, low age at first maturity, high natural mortality and high growth rate. Conversely, species towards the K- end of the spectrum were opposite in these respects. Such conformity, with its dependence on food availability, links these correlates through body size to fecundity. (Because of a commensurate mouth size,

the smaller the teleost the lower the trophic level it exploits. In a food-poor environment like the deep-sea this is an important consideration.) A measure of potential reproductive investment per species is therefore obtainable from species' maximum adult size and maximum fecundity. The gross reproductive investment can then be assessed along phylogenetic lines in relation to vertical/bathymetric distribution and therefore to broad resource categories.

The r- and K- concept in fish life-history styles has been considerably refined by Balon (1988, 1989, 1990). He postulates homeorhetic states of altricial (small eggs, little yolk, smaller less developed young) and precocial (large amount of dense yolk, larger more developed young) life-history styles, which are the cause of evolutionary patterns and relate to a complex classification of reproductive guilds (e.g. Balon 1990). Such direct and indirect developmental alternatives were discussed in detail by Flegler-Balon (1989), who elaborated on specific reproductive parameters for a wide variety of such guilds. She pointed out that indirect development was typified by altricial species, which was especially common among pelagic marine species. Increasing parental care from such egg scatterers to internal bearers resulted in yolkier and less numerous eggs and culminated in direct development. Flegler-Balon (1989) gave a zoarcid and a dasyatid ray as examples of different precocial styles relevant here. While the current investigation concerns largely egg scattering altricial species (see above), general detailed categorization is precluded here by lack of information for most species. Known noteworthy styles, however, are categorized where appropriate.

My investigation was structured from a data base of species' maximum size (weight) for the known pelagic and demersal fishes of the North Atlantic Basin. This provided the phylogenetic composition of the pelagic and demersal ichthyofauna at ordinal and familial rank, together with the means of synthesising the overall species size spectra of the two ichthyofaunal elements. Where available, the maximum fecundity per species was incorporated into the data base for a comparison with species' size classes among the major orders and as a framework for consideration of the various arrangements for maximizing fecundity (e.g. sexual dimorphism, syn-

chronous hermaphroditism, viviparity, 'batch' spawning, seasonal synchrony, egg rafts, parental care, etc.). Finally, species' size and biomass spectra from known populations of pelagic and demersal fishes were used to assess potential basinwide patterns of reproduction. No simple picture of factors explaining the evolution of reproductive arrangements among oceanic fishes emerged. Instead a web of possible correlations is indicated to form a framework for future research.

Materials and methods

For the purposes of this paper the area considered as the North Atlantic Basin extends from the Arctic Basin southward to the equator. It includes the Caribbean and Gulf of Mexico but excludes the Mediterranean Sea. The northerly limit of this region abutts the rim of the Arctic Basin, with its distinct faunistic composition (see Andriyashev 1953 for review). This biogeographic boundary runs from the Hebridean slope edge, along the Wyville Thomson Ridge and Faroe-Iceland Ridge to the Icelandic slopes and across the Denmark Strait to the Greenland slope. The oceanic realm has been taken as that region seaward of the 200 m isobath which broadly marks the shelf-slope break. Thus the pelagic species considered include only those whose geographic ranges extend far beyond the limits of the continental shelf waters. The demersal species taken are those whose depth (sounding) ranges commence at, or extend substantially beyond, the 200 m isobath.

The term demersal is used here to combine both the benthic and benthopelagic categories of deep bottom-living fishes (sensu Marshall & Merrett 1977). The lack of buoyant means in benthic fishes sets them apart with a very different lifestyle from those that are benthopelagic. Nevertheless this group [listed by Marshall & Merrett (1977) as being most: chlorophthalmids, ipnopids, synodontids (Aulopiformes), ogocephalids (Lophiiformes), scorpaenids, cottids (Scorpaeniformes), zoarcids (Perciformes)] form a small proportion of the demersal fauna overall and are widely distributed through all depth zones. Thus they have not been

treated as a separate category, but attention is drawn to them where appropriate.

The inventory of pelagic and demersal oceanic species was culled from a variety of sources, from the literature [notably FNAM (Whitehead et al. 1984, 1986a, b); CLOFETA (Quero et al. 1990a, b); FWNA (Fishes of the western North Atlantic, various editors); Haedrich & Merrett (1988)], unpublished data from Woods Hole Oceanographic Institution (WHOI) midwater trawl samples, the Institute of Oceanographic Sciences Deacon Laboratory's (IOSDL) and my own demersal trawl samples. The inventory was arranged phylogenetically following Nelson (1984).

Distributional differences within both the pelagic and demersal ichthyofaunas were examined by partitioning the data by depth zone. The pelagic fauna was divided into two strata (0–399 m and > 400 m), based upon presumed natural distributional limits of surface-living (epipelagic) fishes and the meso- and bathypelagic forms. The usual concept of the epipelagic layer as a 200 m thick euphotic zone has been broadened here to achieve a more distinct separation between forms associated with the near-surface waters (e.g. tuna) and the truly deep-sea fauna. Subdivision of the lower pelagic zone, although desirable, was impractical owing to the small proportion of species sampled with mouth opening/closing nets. The demersal fauna, on the other hand, could be considered in four strata (200–399 m, 400–1999 m, 2000–3999 m, 4000 + m), conforming with a generalized concept of outer shelf, continental slope, continental rise and abyss. Since vertical ontogenetic descent from epipelagic larvae is commonplace among deep-sea fishes, species were allocated to zones according to their known limits of adolescent-adult depth distribution [daytime distribution in the case of pelagic species]. Species allocation was to the shallowest zone of known abundance, in view of the constraints to distributional knowledge given below. The data were not subdivided geographically.

The great variation in body shape of the species considered dictated that, for comparative purposes with fecundity, length was an unrealistic measure of size. Fish weight was considered more appropriate for such comparison, but is rarely available in the

literature. Some data could be obtained in this way, however, and these were augmented by unpublished Institut für Seefischerei, Hamburg (ISH), International Center for Living Aquatic Resources Management, Manila (ICLARM), Scottish Association for Marine Science (SAMS), Woods Hole Oceanographic Institution (WHOI) and personal data. Maximum sizes attained in the North Atlantic Ocean basin were taken for comparison with maximum known fecundity, to offset bias in sampling techniques and as a measure of potential for each species. In many cases maximum weights were unobtainable and so had to be estimated from length in comparison with species of analogous size and shape. Sizes were grouped into \log_2 classes.

Instantaneous fecundity of a species was taken to be the total number of the most advanced cohort of eggs present in an ovary pair. This overlooks the functional aspects of determinate or indeterminate fecundity, which have not been assessed among deep-sea species. Maximum fecundities were taken, both from the literature and from my unpublished data. Only data originating in the North Atlantic were used, to offset any inter-ocean variation in widely distributed species. Fecundity was reported by number classed according to \log_2 .

A wide variety of limitations are implicit in this study, to caution care in the interpretation of results. Among the main sources of inaccuracy is the likely incompleteness of the inventories of pelagic and demersal species. This is compounded by the 'boundary effect' for species inclusion, at the shelf-slope break and other zonal boundaries chosen. Allocating a species to a single zone on the basis of its overall limit of depth distribution is a somewhat crude approach, since within this range there usually exists a principal distribution layer of maximum density. This is known for such a small proportion of either assemblage, however, that the upper limit of the adolescent-adult distributional range was used here for consistency. It should be pointed out that fish density in the deeper of the two pelagic ichthyofaunal zones considered here is considerably attenuated below about 3000 m. It remains very sparse until some tens of metres above the bottom (IOSDL unpublished data).

Geographic variations in occurrence and depth

range could not be taken into account for most species and so were disregarded. Similarly, intra-specific differences occur in fecundity in some species on an ocean basin scale (Badcock & Merrett 1976, Clarke 1984, Kawaguchi & Mauchline 1987, McKelvie 1989) but, for the majority of species there are no comparative data and so such variation also had to be ignored. The necessary estimation of weight data for so many species is a source of inaccuracy in itself, but this is ameliorated by grouping the data into \log_2 size classes. The maximum size of many species is also open to doubt. In mid-water, especially, sampling has largely been by small nets (with the notable exception of the collections made by the 'Walther Herwig', e.g. see Krefft 1974), where net avoidance by larger specimens must be expected (e.g. Clarke 1973, Clarke & Wagner 1976). Furthermore, according to Childress et al. (1980) mature individuals are so short-lived once they reach maximum size that they comprise only a small fraction of the population at any given time. No attempt has been made to consider lifetime fecundity among those species for which estimates are available. While some of these species are known to be semelparous (spawning once per lifetime), the assumption of iteroparity (repeat spawnings per lifetime) in all the remainder may be unjustified. Fecundity counts give no indication of whether the estimate represents 'all-at-once' (single cohort of eggs spawned together) or 'batch' (several cohorts of eggs spawned sequentially) spawning styles. However,

Table 1. Vertical distribution of oceanic fishes by family and species in the North Atlantic Basin, a – subdivided by major zones with the proportion of families restricted to each indicated; b – subdivisions of the demersal zone.

	Total number of families	Total number of species	Proportion restricted to zone
(a) Pelagic: 0–399 m	28	80	89%
> 400m	66	509	79%
Demersal: total	72	505	78%
(b) 200–399 m	30	74	
Demersal – 400–1999 m	58	347	
by strata: 2000–3999 m	14	64	
> 4000 m	7	20	

wherever possible these aspects are discussed in the accounts of the orders.

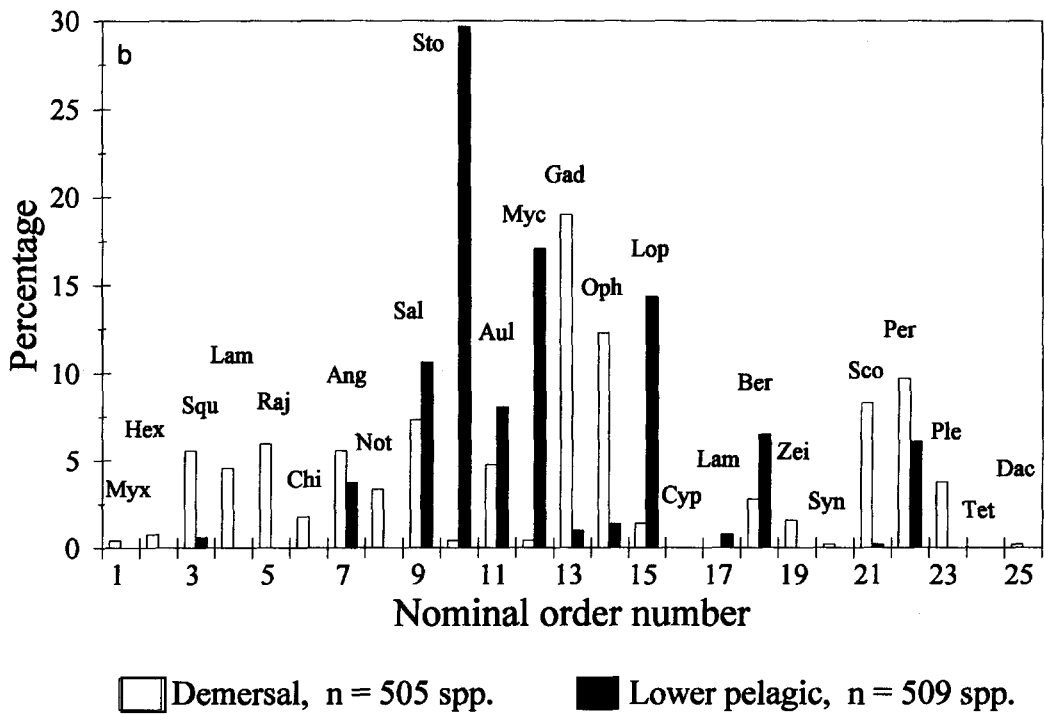
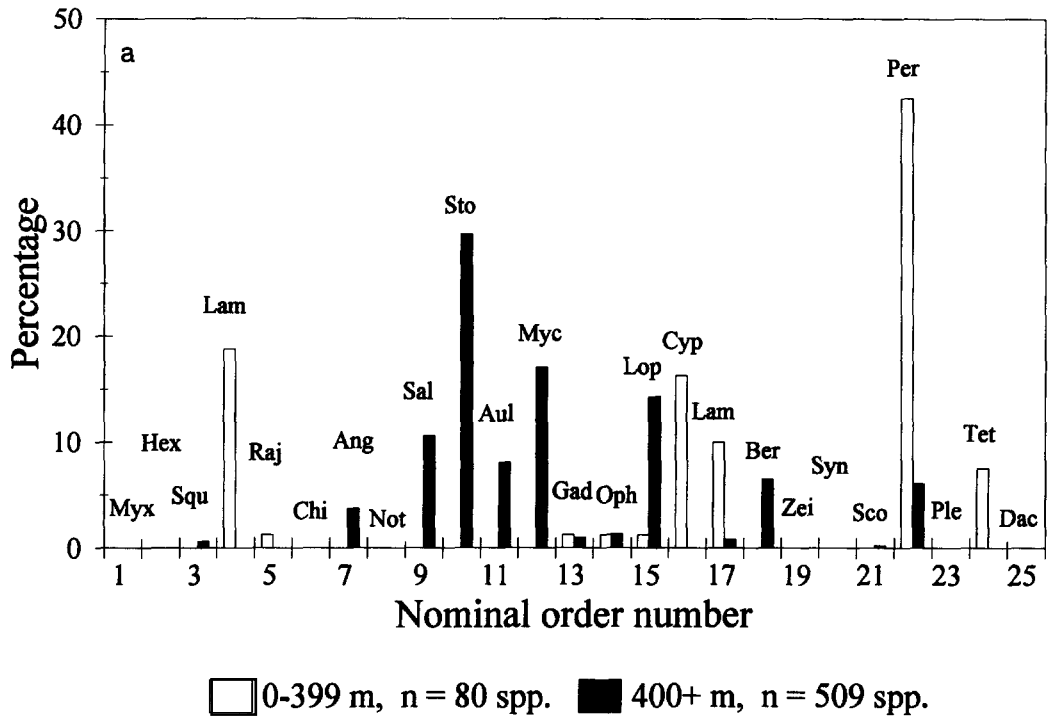
Results and discussion

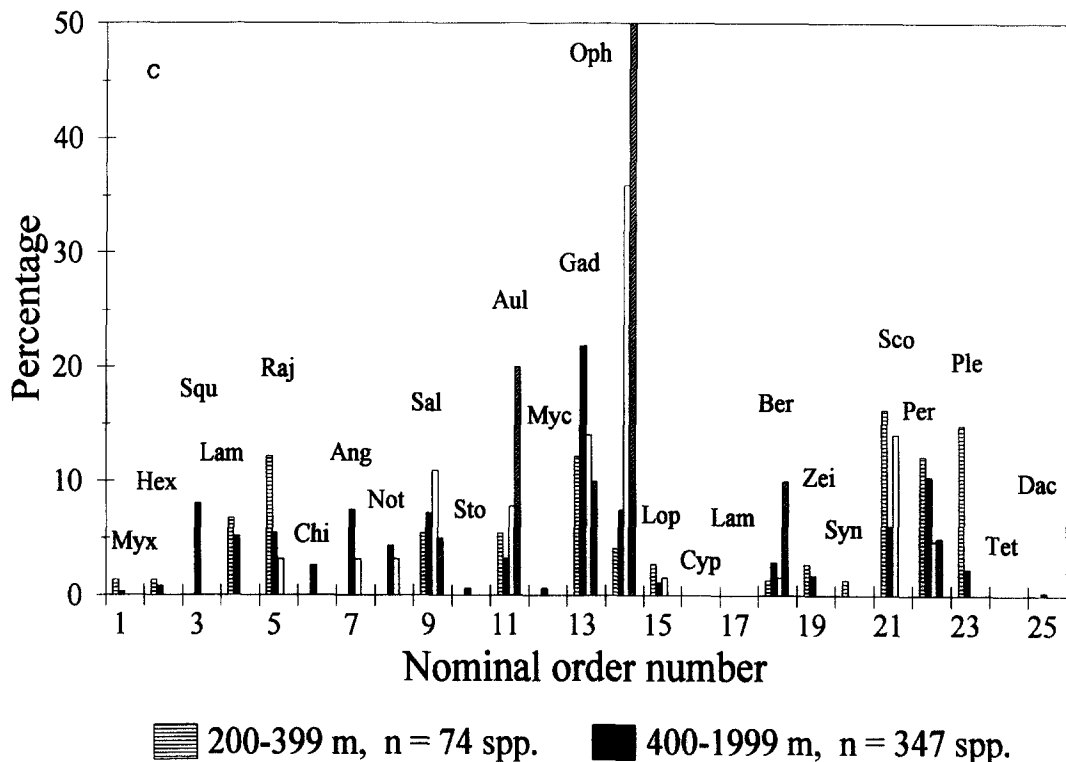
Using the criteria outlined above, the oceanic ichthyofauna of the North Atlantic basin currently stands at 1094 species, representing 143 families and 25 orders. There are rather more pelagic species (589) than demersal (505), distributed among 93 pelagic and 72 demersal families. A remarkably low level of congruity exists at family level among the upper pelagic, lower pelagic (mesopelagic + bathypelagic) and overall demersal zones (Table 1). In all zones more than three quarters of the families are restricted to a single zone, with only the Gempylidae represented in all. Members of this family are often pseudoceanic (e.g. see Merrett 1986) and therefore concentrated around the oceanic rim and oceanic islands (Nakamura & Parin 1993), where zonal intermixing is most likely. Three families occur in both the upper pelagic and the demersal zones, while 13 are common to the lower pelagic and demersal.

Distribution of species within orders

Overall, the demersal assemblage contains more orders (22) than does the pelagic assemblage (18). Moreover, species representation in the upper pelagic zone (0–399 m) contrasts strongly with that of the lower pelagic zone (> 400 m) (Fig. 1a). Dominant in the upper zone are perciform [order no. 22 (see Appendices 1, 2); 43% zonal frequency], lamniform (no. 4; 19%), cyprinodontiform (no. 16; 16%), and lampriform (no. 17; 10%) species. Rajiform (no. 5), lamniform, cyprinodontiform and tetraodontiform (no. 24) species are unreported from the lower pelagic zone.

Again, there is a striking contrast in species representation by order between the lower pelagic and demersal assemblages which, taken together, constitute the true deep-sea fauna (Fig. 1b). Among the lower pelagic assemblage, the dominant orders are the Stomiiformes (no. 10; 29%), Myctophiformes





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 Fig. 1. Relative distribution of species per order among the oceanic fishes of the North Atlantic Basin. a – Pelagic ichthyofauna (589 spp. from two depth zones); b – Comparison of the deep pelagic ichthyofauna (509 spp.) with the demersal (505 spp.); c – depth stratified representation of the demersal ichthyofauna. (Nominal order numbers and labels refer to order listing in Appendix 1.)

(no. 12; 17%) and Lophiiformes (no. 15; 14%). Few orders, besides the Anguilliformes (no. 7; 4%), Salmoniformes (no. 9; 11%), Aulopiformes (no. 11; 9%), Beryciformes (no. 18; 6%) and Perciformes (no. 22; 6%) approach similar species frequency in both assemblages. (Note, however, that the perciform species in the lower pelagic comprise only 6%, in comparison to 43% in the upper pelagic assemblage.) Dominant among the demersal assemblage are gadiform (no. 13; 19%), ophidiiform (no. 14; 12%) and scorpaeniform (benthic – no. 21; 8%) species, as well as the perciform (9%) and salmoniform (7%) species (Fig. 1b). A far greater diversity among the orders represented is evident from the demersal assemblage when compared with the lower pelagic assemblage (22 vs. 13). Thus, apart from three squaliform (no. 3) species, the Agnatha (no. 1) and Chondrichthyes (no. 2, 4–6) are unknown from the lower pelagic, as are the Notacanthiformes (no. 8), Zeiformes (no. 19), Syngnathiformes (no. 20),

Pleuronectiformes (benthic – no. 23) and the Dactylopteriformes (benthic – no. 25).

Bathymetric sub-division of the demersal assemblage indicates differences in ordinal composition with increased depth (Fig. 1c). The frequency of ordinal representation increases from 15 orders in the upper slope zone (200–399 m – a quasi-shelf zone) to 21 orders in the mid-slope zone (400–1999 m). Representation is then much reduced in the rise (2000–3999 m; 11 orders) and abyssal zones (4000 + m; 6 orders). Some of this reduction arises from the evident absence of the Agnatha (no. 1) and chondrichthyes [no. 2–6, with the exception of a small representation of Rajiformes (benthic – no. 5) on the rise] at the two lower levels. Furthermore no demersal Anguilliformes (no. 7) nor Notacanthiformes (no. 8) are found predominantly at abyssal depths. Species' representation within orders is also variable among zones. The percentages of the benthic orders Rajiformes (no. 5; 12.5%), Scorpaeni-

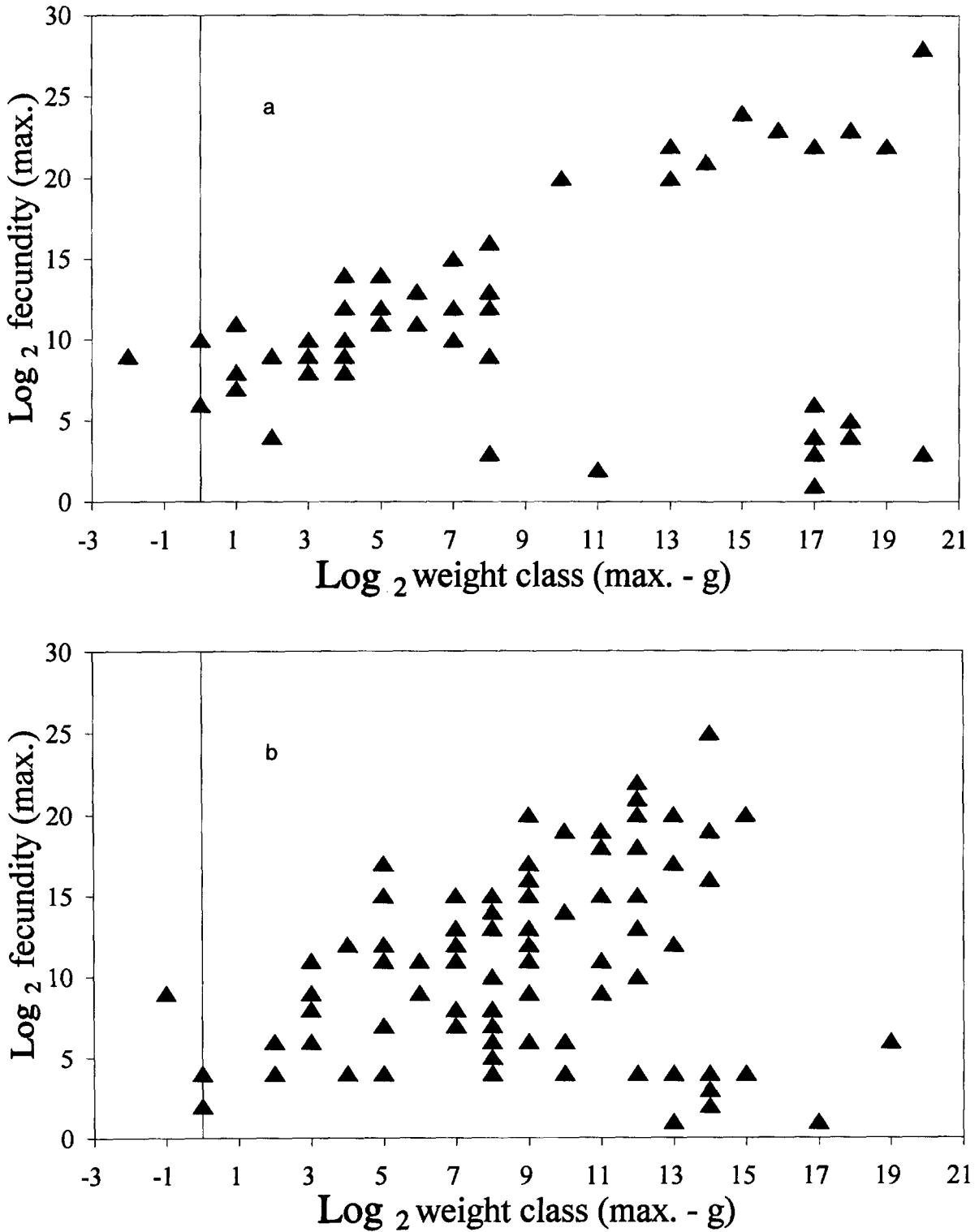


Fig. 2. Relationship between species' maximum fecundity and maximum size among the oceanic fishes of the North Atlantic Basin (log₂ groupings) for a – the pelagic total (n = 60) and b – demersal total (n = 95) ichthyofauna.

formes (no. 21; 16.7%) and Pleuronectiformes (no. 23; 15.2%) are higher on the upper slope than elsewhere. The Squaliformes (no. 3; 8.1%) are concentrated in the mid-slope zone, where the Anguilliformes (no. 7; 7.6%) and the Gadiformes (no. 13; 22.1%) peak also. The Salmoniformes (no. 9; 10.9%) reach their highest proportion in the rise zone, where the Ophidiiformes (no. 14; 35.9%) and the Scorpaeniformes (no. 21; 14.1% – all family Liparidae) are also important. While the numbers of species centred in the abyssal zone are low (20), the Ophidiiformes (no. 14; 50%), Aulopiformes (benthic – no. 11; 20%) and Beryciformes (no. 18; 10%) all assume their highest proportions at this level.

By excluding the predominantly secondary deep-water fauna of the upper pelagic zone and the Arctic Basin from consideration, it appears that Andriyashev's (1953) primary ancient deep-water fauna of the oceanic North Atlantic Basin can therefore be further sub-divided on the basis of the above evidence. Sufficient differences are apparent at the ordinal level between the demersal and lower pelagic assemblages, and also among the bathymetrically sub-divided demersal assemblage, of the overall ichthyofauna to suggest that specialization and divergence probably occurred early on in the colonization of the deep-sea by fishes (Fig. 1b, c).

Body size and its relationship to fecundity among the major orders represented in the North Atlantic Basin

Fecundity data are available for some 10% and 19%, respectively, of the pelagic and demersal ichthyofauna currently listed for the North Atlantic Basin. Despite this low proportion, apparently similar trends are evident from the total representation of both assemblages. As expected, the majority of species (pelagic spawners) display a positive relation between (maximum) fecundity and (maximum) body mass (Fig. 2a, b). This observation agrees with those from other assemblages (e.g. neritic and freshwater, Duarte & Alcaraz 1989). The regressions of \log_2 fecundity against \log_2 weight derived from various orders comprise the general relationship (Anguilliformes/Notacanthiformes,

Salmoniformes/Aulopiformes, Stomiiformes, Myctophiformes, Gadiformes – Fig. 8, 9, 4, 5, 10), however, all differ significantly from one another at least to the 0.05 level. This suggests a phylogenetic element to the overall scatter plots (Fig. 2), but subject to the constraints of the fecundity data given above. In Fig. 2a, b another group can be identified whose fecundity is evidently independent of body mass. These comprise the live-bearing chondrichthyans and the large egg/low fecundity, benthic spawning teleosts.

The aim here is to consider the arrangement of data from the major orders and/or families within the overall fecundity/body size distribution. Thus any emergent pattern can be related to what is known about species' reproductive styles and relative abundance on a basin-wide scale.

Pelagic representatives

Chondrichthyes

Squaliformes. – Pelagic squaloids are represented by relatively few species in the North Atlantic and these occur largely at mesopelagic levels (weight range 2^8 to 2^{11} g; Appendix 1b). At the bottom of the range is *Squaliolus laticaudus* (ref. no. 14 – Fig. 3), possibly the smallest known shark (Compagno 1984). All pelagic squaloids are smaller than their demersal counterparts. They are all ovoviviparous (sensu Heemstra & Greenwood 1992; specifically the 'yolksac viviparity' reproductive style of Compagno 1990) with low fecundity in the range 2^2 to 2^3 young (Fig. 3). Compagno (1984a, b, 1990) gave their reproductive details, so far as these are known, and discussed this style within the reproductive phylogenetic progression.

Lamniformes. – This group of pelagic sharks comprises large, top predators. Their representation in the oceanic realm of the North Atlantic is within the weight range 2^{11} to 2^{25} g (Appendix 1a). Despite their size, they have low fecundity (2^1 to 2^6 eggs; Fig. 3) and depend on large offspring size attained through ovoviviparity to counter juvenile mortality.

The order Lamniformes of Nelson (1984) encompasses several orders in the classification of Com-

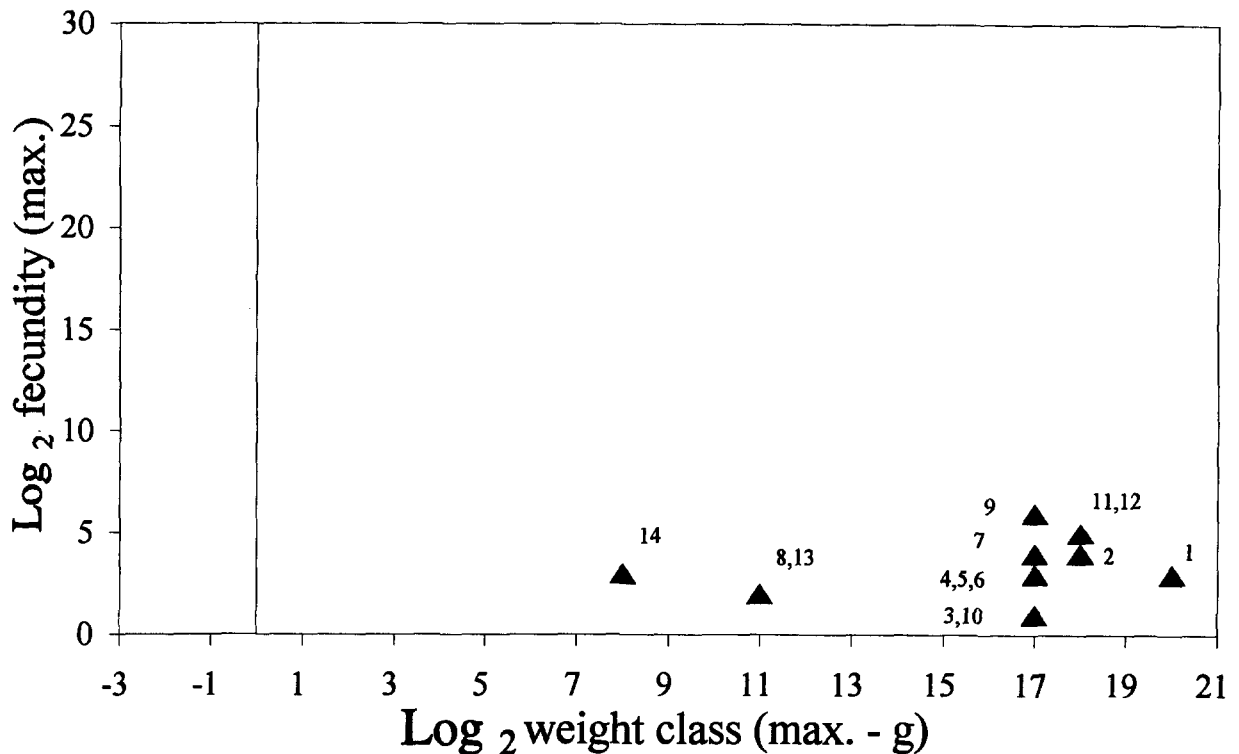


Fig. 3. Relationship between species' maximum fecundity and maximum size among the pelagic oceanic sharks ($n = 14$; orders Squaliformes and Lamniformes) of the North Atlantic Basin (\log_2 groupings). (Species are identified by number from Appendix 3a).

pagno (1984a, 1990), with those species found in the North Atlantic Basin being grouped into the orders Orectolobiformes, Lamniformes and Carcharhiniformes. It is instructive to consider detailed reproductive arrangements according to Compagno's (1990) scheme. Thus the single orectolobiform species represented, the world's largest living fish, the whale shark *Rhincodon typus*, may be oviparous (Compagno 1984). The lamniforms and carcharhiniforms, however, are viviparous. Development in all lamniforms is by what Compagno (1990) termed 'cannibal viviparity' and in the carcharhiniforms represented by 'placental viviparity'. Compagno (1990) considered both styles phylogenetically derived and discussed these specializations in detail.

Osteichthyes

Stomiiformes. – This is the most speciose order among the pelagic fishes of the North Atlantic (Fig. 1a), with peak representation in the weight range 2^4 to 2^8 g (Fig. 4, Appendix 1b). Fecundity estimates

are available for only a few species representing the smaller end of the size class range. The known reproductive arrangements in this group are complex. Several species are 'batch' spawners [e.g. *Valenciennellus tripunctulatus* (ref. no. 21 – Fig. 4) – Badcock & Merrett 1976, Howell & Krueger 1987], some are semelparous [*Cyclothone braueri* (ref. no. 16 – Fig. 4) – Badcock & Merrett 1976, *C. alba* (ref. no. 15 – Fig. 4) – Miya & Nemoto 1986b], while others are wholly or partially protandrous hermaphrodites [*C. microdon* (ref. no. 17 – Fig. 4) – Badcock & Merrett 1976, *Gonostoma bathyphilum* – Badcock 1986, *G. elongatum* – Fisher 1983]. Clarke (1983) reported that most central Pacific Stomiiformes were sexually dimorphic in size or abundance. Sexual dimorphism in size is evident among some North Atlantic species [e.g. *Argyropelecus hemigymnus* (ref. no. 24 – Fig. 4), *Argyropelecus aculeatus*, *Valenciennellus tripunctulatus* – Howell & Krueger 1987, *Cyclothone braueri*, *C. pseudopallida* (ref. no. 19, Fig. 4), *C. pallida* (ref. no. 18 – Fig. 4) – Badcock & Merrett

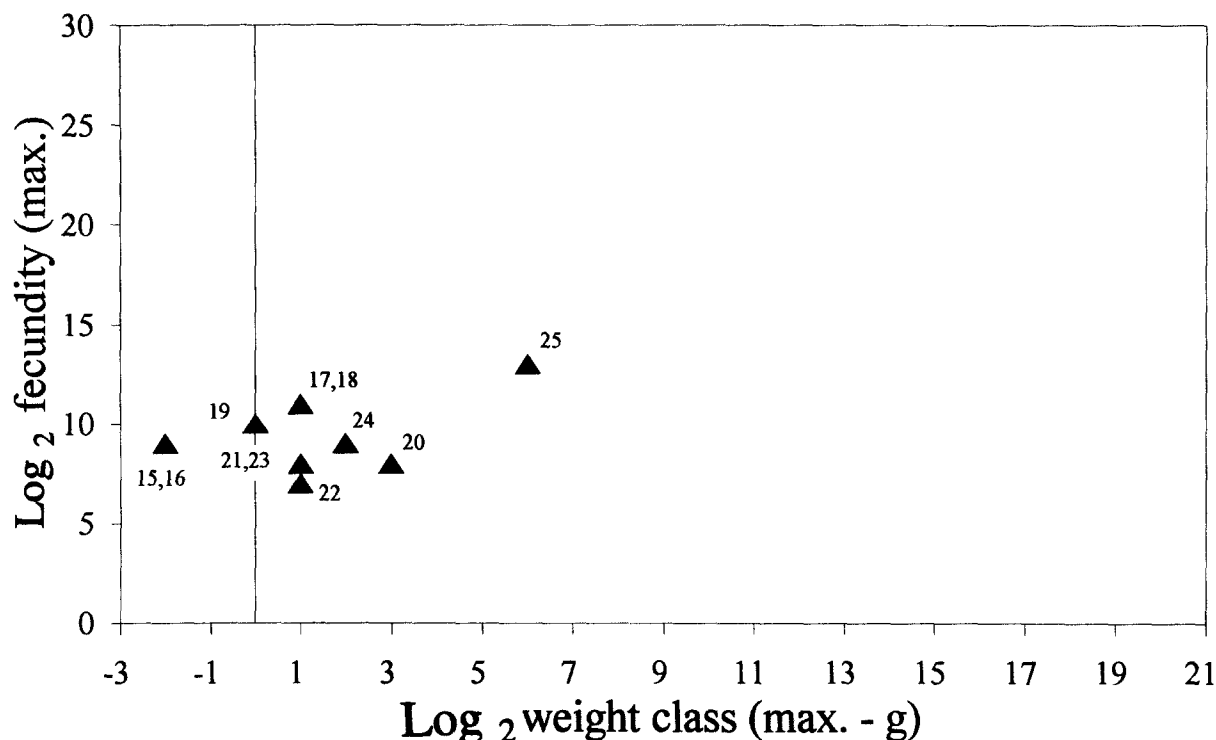


Fig. 4. Relationship between species' maximum fecundity and maximum size among the pelagic oceanic representatives of the order Stomiiformes ($n = 11$) of the North Atlantic Basin (\log_2 groupings - fecundity = $8.99 + 0.34$ weight; $r^2 = 0.19$). (Species are identified by number from Appendix 3a).

1976, *Idiacanthus fasciola* (ref. no. 25 - Fig. 4) - Beebe 1934, *Stomias* spp. Gibbs 1969]. Sexual differences in depth distribution and abundance were noted among North Atlantic *Cyclothone* by Badcock & Merrett (1976). Females in the more advanced stages of maturity were caught deeper than males and less advanced females in *C. braueri*, *C. microdon* and *C. pallida*. In *C. braueri*, the overall sex ratio was skewed in favour of females in depths where the highest proportion of running ripe females occurred. Yet a higher proportion of males were ripe (identified by advanced nasal rosette development) in this part of the distributional range.

Marshall (1984) concluded that semelparity in mesopelagic *Cyclothone* was an adaptive feature accompanying pedomorphism. He contrasted their non-migrant life-style with their rapidly growing competitors, the lanternfishes. He concluded that without such a tendency, a two-year life cycle of *Cyclothone* might be too costly in terms of mortality

to sustain its life history. Furthermore, Marshall pointed out that the bathypelagic, protandric *C. microdon* is substantially more fecund than the mesopelagic, semelparous *C. braueri*. He related this to both size and relative abundance, a feature that will be returned to later. Miya & Nemoto (1991) expanded on this theme and noted that protandry was a means of maintaining high fecundity under food-poor conditions.

Myctophiformes. - Most lanternfishes are nocturnal vertical migrants and together have by far the greatest biomass of any midwater fish group (Marshall 1984). Yet their individual adult size is generally small. The North Atlantic representatives are largely embraced by the weight range 2^3 to 2^7 g and fecundity range 2^6 to 2^{15} eggs (Fig. 5, Appendix 1b). Most species are short-lived. Karnella (1987) commented on the longevity of 28 of the 63 species of myctophids sampled in Ocean Acre, off Bermuda.

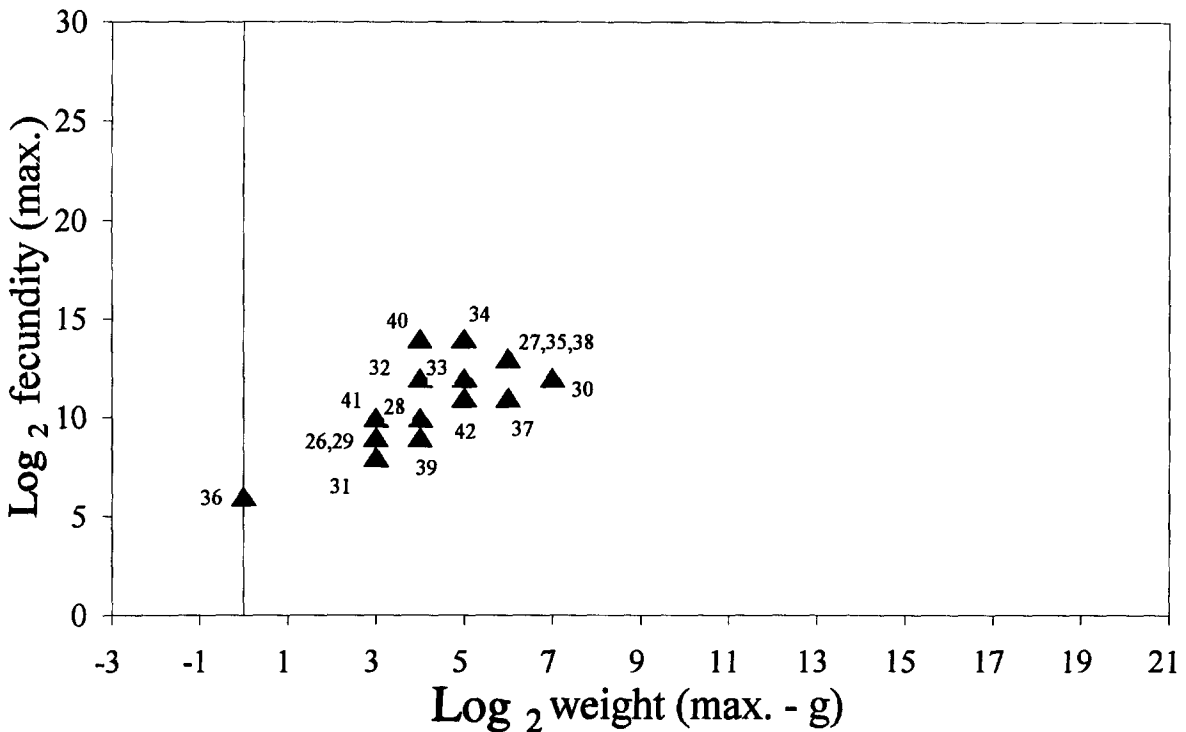


Fig. 5. Relationship between species' maximum fecundity and maximum size among the pelagic oceanic representatives of the order Myctophiformes ($n = 17$) of the North Atlantic Basin (\log_2 groupings - fecundity = $6.45 + 1.03$ weight; $r^2 = 0.60$). (Species are identified by number from Appendix 3a).

Of these 54% (15) were annual species, 32% (9) had a 2-year life span and only 14% (4) lived longer than 2 years. As in the case of some stomiiforms, some Pacific myctophid females are either larger or more abundant than males, so that the biomass of mature females in the populations is greater than that of mature males (Clarke 1983). In Atlantic collections from off Bermuda, Karnella (1987) found skewed sex ratios among four of the 13 most abundant species, all in favour of males. Yet, in some 7 of these species, females were found to grow to a larger size than males, an observation in agreement with the Pacific data. In addition, sexual dimorphism is widely expressed in additional luminous tissue and organs borne by male lanternfish (see Nafpaktitis et al. 1977, Kawaguchi & Mauchline 1982). It is noteworthy, however, that while such caudal sexual dimorphism is the norm among the subfamily Myctophinae, it is rarely found in the subfamily Lampantinae (Paxton 1972). There is no correlation with

either size or fecundity between these two subfamilies in the North Atlantic data.

Miscellaneous species. - Included in the plot of miscellaneous species are the scombroid fishes, an important group of 'higher' teleosts. These are large (weight range 2^{13} to 2^{19} g, Fig. 6), highly fecund (range 2^{21} to 2^{24} eggs), epipelagic predators. The remaining species represent widely differing categories. At one extreme is one of two pelagic teleosts known to be live-bearers [Parabrotulidae: *Parabrotula plagiophthalma* (ref. no. 51 - Fig. 6), 2^2 g, 2^4 eggs resulting in the birth of advanced young and categorizing the species as a 'histotrophic livebearer' in the scheme of Balon (1990) from evidence of trophotaeniae observed by Turner (1936), discussed in Wourms & Cohen (1975); sexually dimorphic in size, with the smaller males producing spermatozoa as a possible adaptation to low density in a pelagic environment (Nielsen 1968, Nielsen et al. 1990)]. At the other is the gigantic and highly fe-

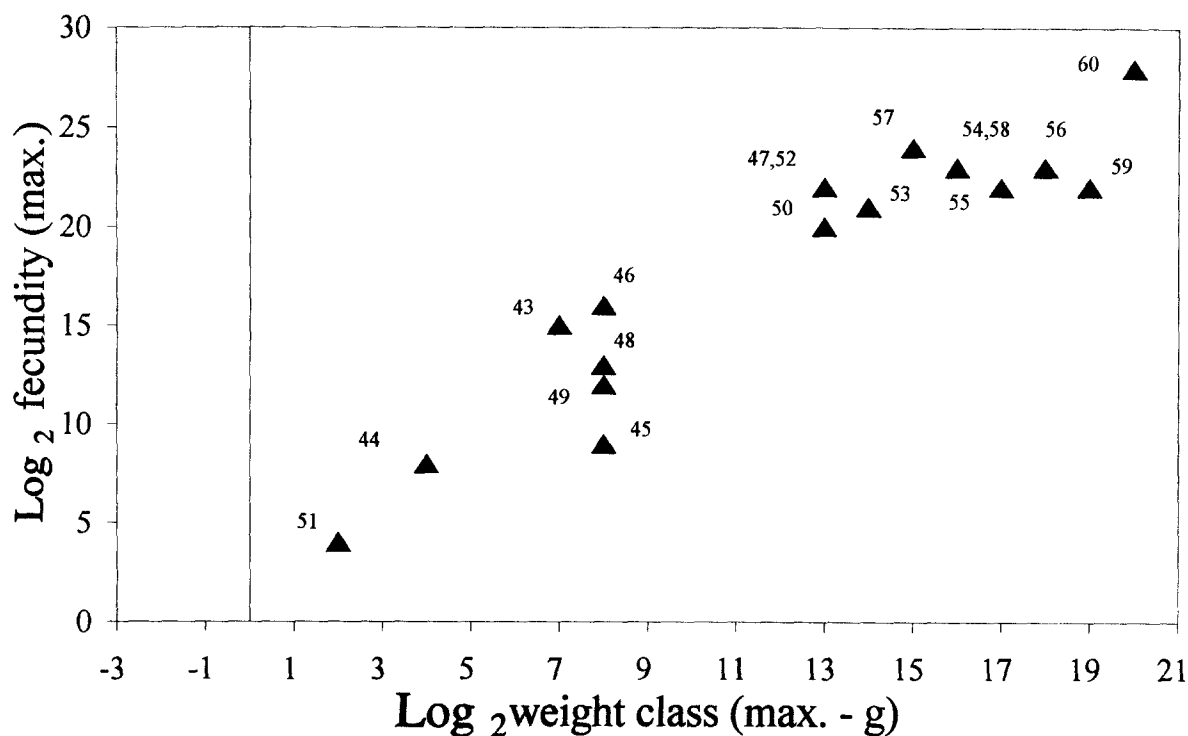


Fig. 6. Relationship between species' maximum fecundity and maximum size among miscellaneous pelagic oceanic representatives of the orders Anguilliformes, Salmoniformes, Gadiformes, Lophiiformes, Cyprinodontiformes and Perciformes ($n = 18$) of the North Atlantic Basin (\log_2 groupings). (Species are identified by number from Appendix 3a).

cund ocean sunfish [Molidae: *Mola mola* (ref. no. 60 – Fig. 6), weight 2^{20} g, fecundity 2^{28} eggs]. Intermediate in fecundity are *Monognathus taaningi* (ref. no. 44 – Fig. 6) and the gulper eel, *Eurypharynx pelecanoides* (ref. no. 43 – Fig. 6), which, together with the nemichthyids and saccopharyngids, are semelparous and display considerable sexually dimorphic changes with increasing ripeness (Nielsen & Smith 1978, Gartner 1983, Nielsen & Bertelsen 1985, Bertelsen & Nielsen 1987, Nielsen et al. 1989). While fecundity is known for only two of the 100 or so species of ceratioid anglerfishes [*Ceratias holboelli* (ref. no. 47 – Fig. 6) and *Haplophryne mollis* (ref. no. 48 – Fig. 6)], the reproductive adaptations of this suborder are striking. Pietsch (1976) reviewed ceratioid reproductive styles and stated, 'they (ceratioids) are most strikingly characterized by having an extreme sexual dimorphism in which males are dwarfed and, in some species, become parasitically attached to the body of a relatively gigantic female'. Egg protection may be a further aspect of ceratioid

style, based on evidence that the egg clutch is embedded in a mucous sheet in at least one species (*Lionophryne arborifera* – Bertelsen 1980). Such an 'egg veil' is also produced in the shelf and upper slope genus *Lophius*, indicating that this is likely to be a phylogenetic, rather than an environmental, adaptation. In the classification of reproductive guilds devised by Balon (1990), such a mode could perhaps be aligned with 'froth nesters' although evidence of guarding is unknown.

Demersal representatives

Chondrichthyes. – Knowledge of this group is restricted to the demersal sharks representing the orders Hexanchiformes, Squaliformes and Lamniiformes. They are comprised of species with maximum sizes within the weight range 2^7 to 2^{20} g (Appendix 2a, b). In common with the pelagic sharks, their demersal counterparts included here are all

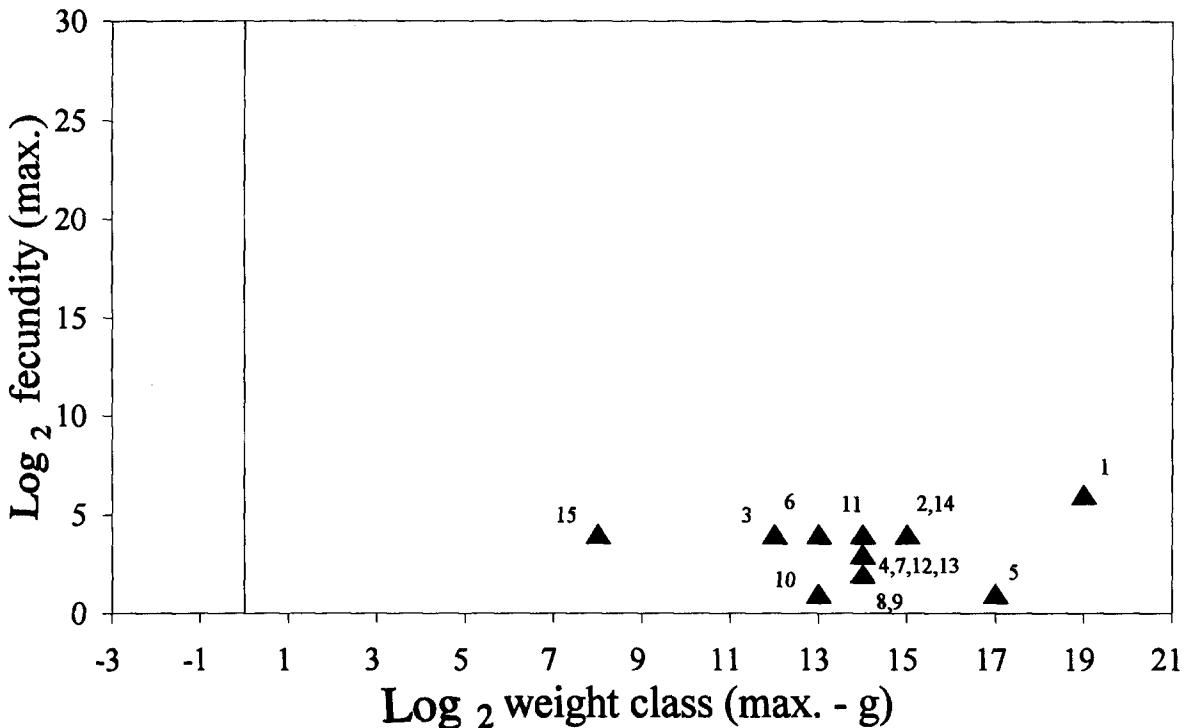


Fig. 7. Relationship between species' maximum fecundity and maximum size among the demersal oceanic sharks ($n = 15$; orders Hexanchiformes, Lamniformes and Squaliformes) of the North Atlantic Basin (\log_2 groupings). (Species are identified by number from Appendix 3b).

ovoviviparous. They all have typically low fecundity (range 2^1 to 2^4 (2^6) young – Fig. 7), demonstrating again the size independent nature of fecundity in this group of fishes. The details of their ovoviviparity are given by Compagno (1990). The Hexanchidae, Chlamydoselachiidae and Squalidae all utilize 'yolksac viviparity', while the lamniforms Odontaspidae, Mitsukurinidae and probably Pseudotriakidae (see Yano 1992) utilize 'viviparous cannibalism'. Unrepresented in Figure 7 are those chondrichthyans (Scyliorhinidae, Rajiformes and Chimaeriformes) which according to Compagno (1990) undergo 'extended oviparity', but for which there are as yet no fecundity data available for North Atlantic species.

Anguilliformes. – Demersal anguilliforms are represented by the family Synphobranchidae, whose members span a substantial size range (2^4 to 2^{13} g; Appendix 2b, c). Fecundity estimates are few, but counts are available for *Synphobranchus kaupi*

(ref. no. 18 – Fig. 8), the dominant species of the slopes of the North Atlantic Basin (see Haedrich & Merrett 1988, 1990). In relation to its rise/abyssal relative, *Histiobranchus bathybius* (ref. no. 16 – Fig. 8), it is of smaller size and lower fecundity. Bruun (1937) traced the development of *S. kaupi* as a leptocephalus larva from an origin in the Sargasso Sea, implying a semelparous life history. The pattern in *H. bathybius* is unknown, although the presence of ripening females over a wide size range (575–1370 mm standard length (SL), personal observation) suggests possible iteroparity. This is supported by the capture of two recently spent females (1330 and 1370 mm SL) at 4580–4540 m in 21° N, 31° W (September–October, 1993 – personal observation). Neither of these fish exhibited obvious morphological degeneration typical of semelparous eels (e.g. Nielsen & Bertelsen 1985, Nielsen & Smith 1978).

Notacanthiformes. – While the largest notacanth

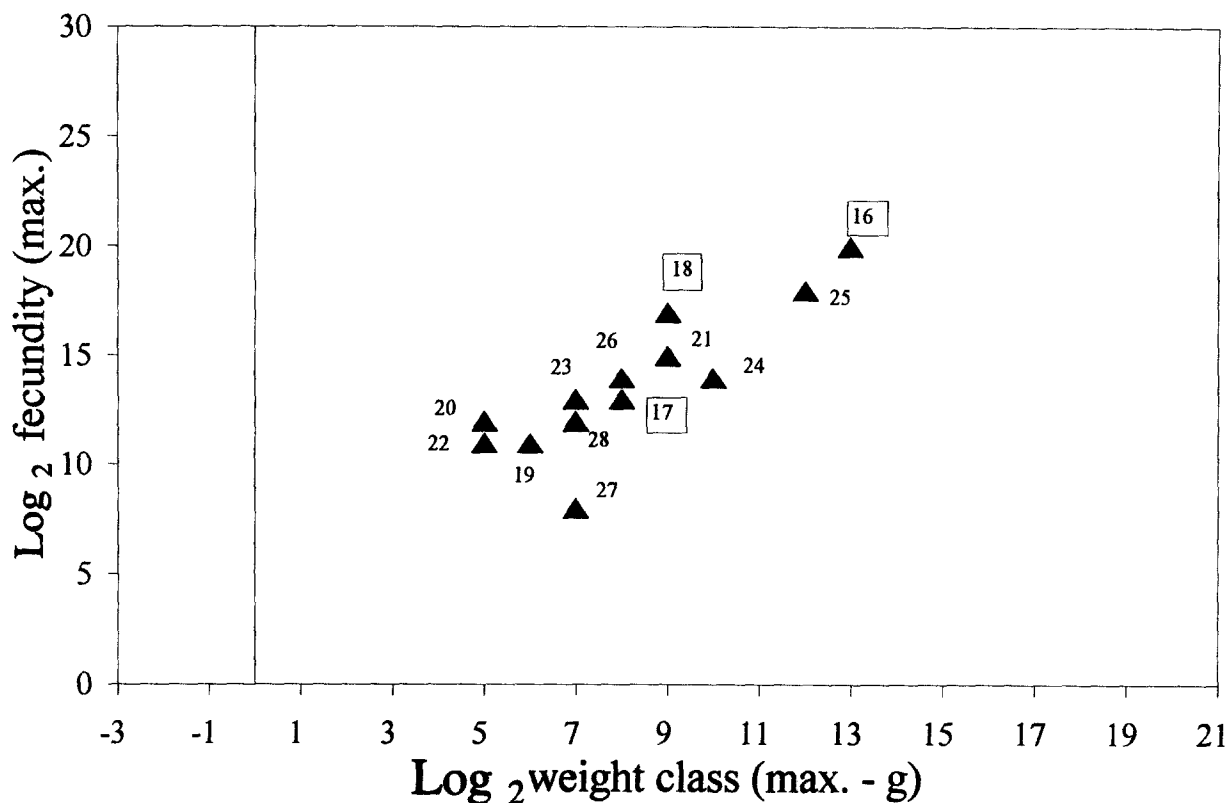


Fig. 8. Relationship between species' maximum fecundity and maximum size among the demersal oceanic eels, halosaurs and spiny eels of the orders Anguilliformes (boxed ref. numbers) and Notacanthiformes ($n = 13$) of the North Atlantic Basin (\log_2 groupings - fecundity (combined) = $4.52 + 1.12$ weight; $r^2 = 0.73$). (Species are identified by number from Appendix 3b).

are of similar size to the largest synphobranchids, the peak in their size frequency distribution is narrower and at smaller size (range 2^4 to 2^{12} g, peak 2^4 to 2^7 g; Appendix 2b, c). Few details are available on their reproductive arrangements; what is known suggests that they are iteroparous 'all-at-once' spawners. Crabtree et al. (1985) have shown that females predominate in populations of *Polyacanthonotus merretti* (ref. no. 27 - Fig. 8), *P. rissoanus* (ref. no. 28 - Fig. 8) and *P. challengerii* (ref. no. 26 - Fig. 8). Sulak demonstrated a similar skewing of the sex ratio in favour of females in four species of the halosaur, *Aldrovandia*. Olfactory sexual dimorphism has been reported in both notacanth and halosaurs and may be typical of breeding males of notacanthiform fishes (McDowell 1973, Sulak 1977, Crabtree et al. 1985). Among those species whose fecundities are plotted here, *P. rissoanus* and *Notacanthus bonapartei* (ref. no. 24 - Fig. 8) are ranking species on

the slope, while *Halosauropsis macrochir* (ref. no. 21 - Fig. 8) is a ranking species on the lower slope and rise in the Porcupine Seabight region of the eastern North Atlantic (Merrett et al. 1991a, b).

Salmoniformes. - The dominant salmoniformes in the deep North Atlantic are members of the family Alepocephalidae. Together they cover a wide size range (2^4 to 2^{13} g; Appendix 2a-d). All known ripe ovarian eggs are large, (2)3 to 4(8) mm in diameter (Golovan & Pakhorukov 1984, Crabtree & Sulak 1986, personal observation), deposited sometimes in batches and sometimes synchronously by implication from multi-modal size frequencies in ripe ovaries in some species. The large eggs size suggests direct development and a precocial life-history style (Flegler-Balon 1989). This is reflected in the placement of the family in the general trend of size-related fecundity (Fig. 9, cf. Fig. 2b). It is notewor-

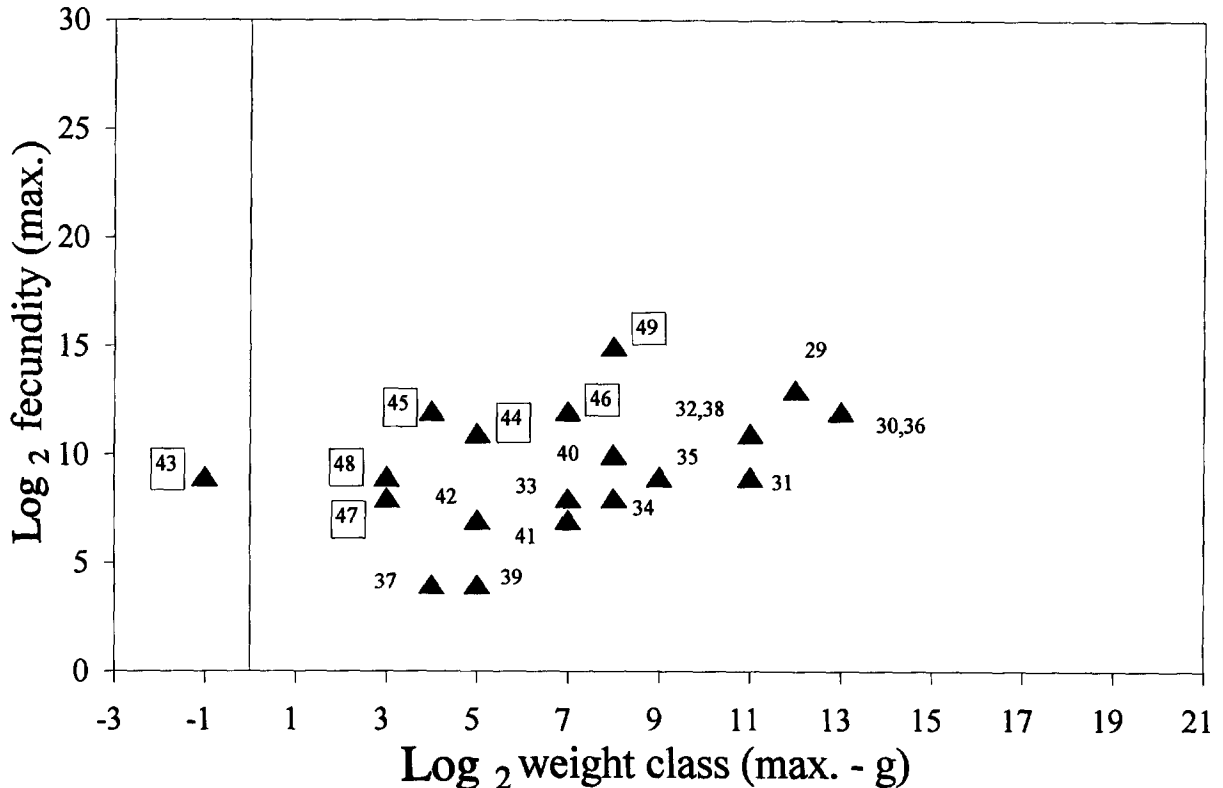


Fig. 9. Relationship between species' maximum fecundity and maximum size among the demersal oceanic representatives of the orders Salmoniformes and Aulopiformes ($n = 21$; boxed ref. numbers) of the North Atlantic Basin (\log_2 groupings – Salmoniformes: fecundity = $1.16 + 0.87$ weight; $r^2 = 0.86$; Aulopiformes: fecundity = $9.08 + 0.20$ weight; $r^2 = 0.09$). (Species are identified by number from Appendix 3b).

thy that success measured by relative numerical abundance is not necessarily correlated with high fecundity in Salmoniformes. In the Porcupine Seabight area, *Alepocephalus bairdi* (ref. no. 30 – Fig. 9) and *A. rostratus* (ref. no. 32 – Fig. 9) dominate on the slope and are relatively highly fecund. *Rinoctes nasutus* (ref. no. 39 – Fig. 9), on the other hand, ranks as a dominant at abyssal depths but with very modest fecundity (Merrett et al. 1991a, b). Crabtree & Sulak (1986) reviewed what is known about alepocephalid reproduction in a consideration of the biology of *Conocara*.

Aulopiformes. – Overall, deep demersal aulopiforms from the North Atlantic are represented by benthic fishes from a wide range of sizes (2^1 to 2^{13} g; Appendix 2a–d). Available fecundity counts from the area, however, are restricted in all but one case [*Bathysaurus ferox* (ref. no. 49 – Fig. 9) – Synodontidae] to the family Ipnopidae (sensu Hartel & Stiass-

ny 1986) (Fig. 9). All are synchronous hermaphrodites, enabling them to maximize fecundity potential in their sparse populations and relatively immobile, benthic life-style. Some, certainly, are 'batch' spawners [*Ipnops meadi*, *Bathymicrops regis* (ref. no. 43 – Fig. 9); Nielsen 1966, Nielsen & Merrett 1993]. Moreover, ipnopid species of small adult size are more dominant among abyssal demersal populations beneath oligotrophic surface waters (*B. regis*) than they are beneath eutrophic surface conditions [*Bathypterois longipes* (ref. no. 44 – Fig. 9)] (Merrett 1987, 1992).

Gadiformes. – The order Gadiformes is the most speciose among deep demersal fishes in the North Atlantic basin (Fig. 1b) and is represented by a wide range of size classes (2^1 to 2^{14} g; Appendix 2a–d). While the family Macrouridae has the greatest species richness among demersal fishes around the oceanic rim (continental slope and rise) of the

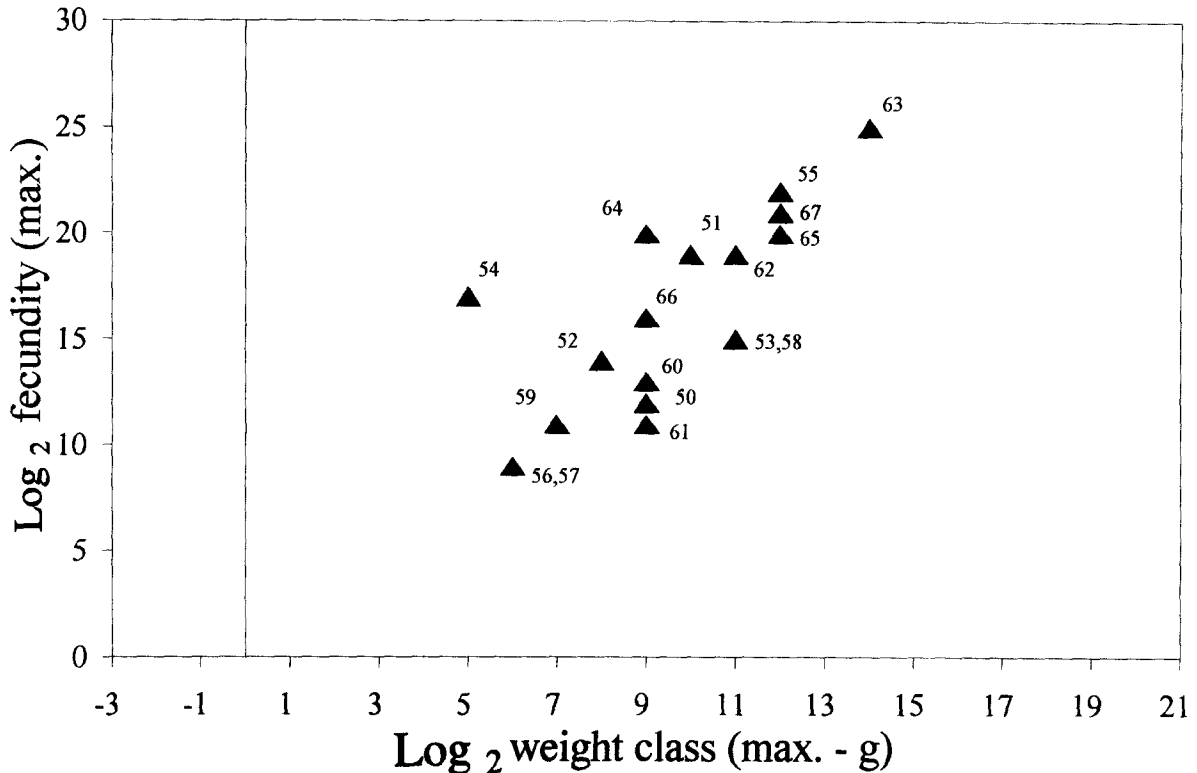


Fig. 10. Relationship between species' maximum fecundity and maximum size among the demersal oceanic representatives of the order Gadiformes ($n = 18$) of the North Atlantic Basin (\log_2 groupings – fecundity = $2.37 + 1.44$ weight; $r^2 = 0.56$). (Species are identified by number from Appendix 3b).

world ocean, the majority are smaller and less fecund than other oceanic gadiforms (Fig. 10). As pointed out above, there seems little relationship between size/fecundity and numerical abundance. *Coryphaenoides (N.) armatus* (ref. no. 55 – Fig. 10) is a highly fecund species (a possible semelparous spawner – Stein 1985) dominating on the rise and abyss beneath eutrophic surface conditions. In the eastern North Atlantic it is sexually dimorphic in size (females larger than males) and abundance, with sex ratios weighted in favour of females (Merrett 1992). *Echinomacrurus mollis* (ref. no. 56 – Fig. 10) is a ranking species ('batch' spawner – Merrett 1987) beneath oligotrophic surface waters (Haedrich & Merrett 1988, 1990, Merrett 1987, 1992, Merrett et al. 1991b). Both *C. (C.) rupestris* (ref. no. 53 – Fig. 10) and *Macrourus berglax* (ref. no. 58 – Fig. 10) are commercially exploited species of medium size and fecundity. *Nezumia aequalis* (ref. no. 59 – Fig. 10

– 'batch' spawner) and *C. (C.) guentheri* (ref. no. 52 – Fig. 10) are small species ranking high in relative abundance on the mid-slope and lower slope-rise, respectively (Merrett et al. 1991a, b), but with relatively modest fecundity (Fig. 10). Another species of small adult size but with contrasting high fecundity is *C. (Lionurus) carapinus* (ref. no. 54 – Fig. 10). This is a ranking species on the continental rise. Haedrich & Polloni (1976) report a small egg diameter (0.5 mm) in this species relative to *N. aequalis* and *C. (C.) guentheri* (1.6 mm and 0.8–0.9 mm, respectively, personal observation). Merrett (1989) showed that macrourids, at least, underwent a transitory ontogeny with a vestige of a larva called an alevin. Adult males in reproductive condition of several species of the Macrouridae are macrosomatic, with enlarged nasal rosettes as in the notacanthids (see above).

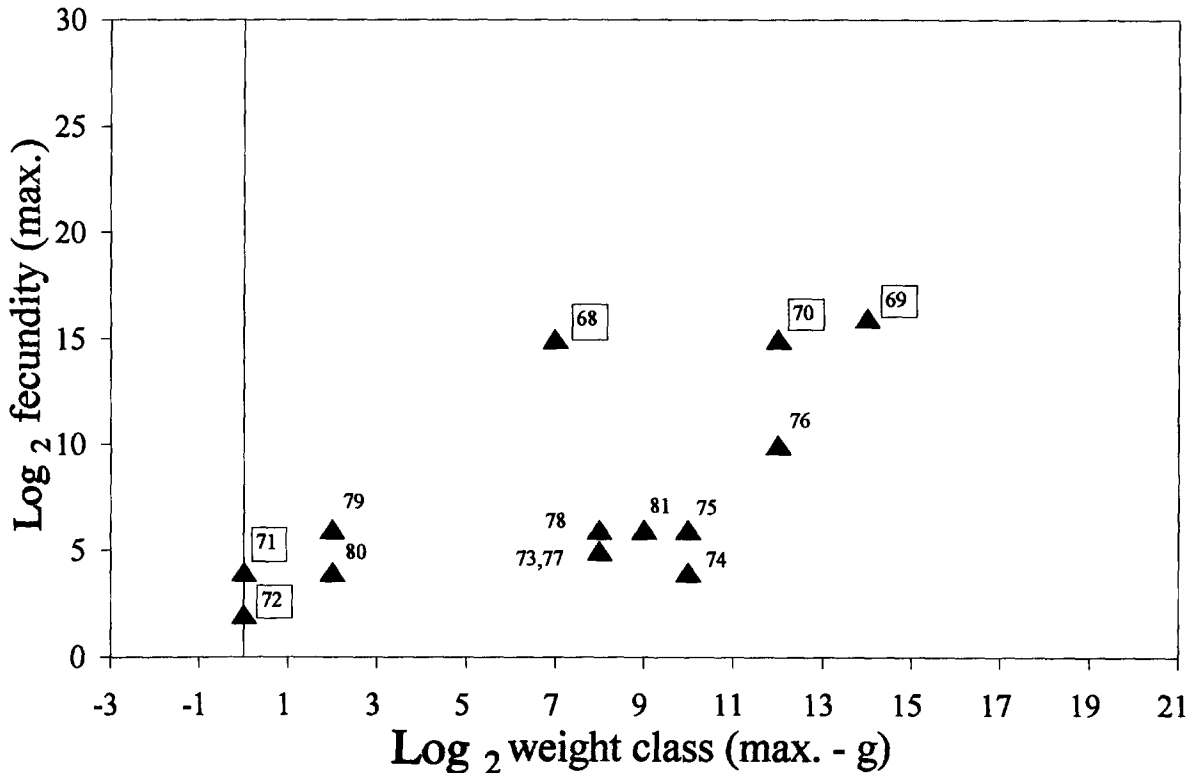


Fig. 11. Relationship between species' maximum fecundity and maximum size among the demersal oceanic representatives of the orders Ophidiiformes (boxed ref. numbers) and Perciformes (Zoarcidae) ($n = 14$) of the North Atlantic Basin (\log_2 groupings). (Species are identified by number from Appendix 3b).

Ophidiiformes. – Knowledge of fecundity within this group, which spans a substantial size range (2^0 to 2^{14} g; Appendix 2 a–d), is poor. The two suborders within the order Ophidiiformes are in part distinguished by their reproductive arrangements. The Ophidioidei are oviparous fishes, while the Bythitoidei are ovoviviparous, a style confirmed by the presence of an intromittent organ in males (Cohen & Nielsen 1978). Spermatophores found in a range of species within the latter group are believed to function in a storage capacity. This is a valuable feature among an apparently sparsely distributed group (Nielsen et al. 1968). Known fecundity among bythitoid females varied widely. In the small, seemingly paedomorphic, family Aphyonidae up to three relatively large clutches of eggs may be distinguished within the ovary, although the number of developing embryos found is in the range 2^2 to 2^4 (Nielsen 1969) (Fig. 11). Conversely,

in the bythitoid species *Cataetyx laticeps* (ref. no. 70 – Fig. 11), much larger adult size coupled with evident parturition in the free embryo (yolk-sac) phase, results in a fecundity in one example of 2^{15} embryos. Such a fecundity is comparable with that of known oviparous ophidioids (Fig. 11).

The advanced development of the free embryos found in the Aphyonidae (Nielsen 1969), coupled with the evidence provided by Wourms & Cohen (1975) that embryos of the related bythitid, *Oligopus longhursti*, possessed trophotaeniae, suggests that they too might be classified as 'histotrophic live bearers' in the reproductive guilds of Balon (1990). *Cataetyx laticeps*, on the other hand, is clearly classed as an 'obligate lecithotrophic live bearer'.

Perciformes – Zoarcidae. – While fecundity data are sparsely represented in Perciformes in general and in zoarcids in particular (Appendix 2a–d), a differ-

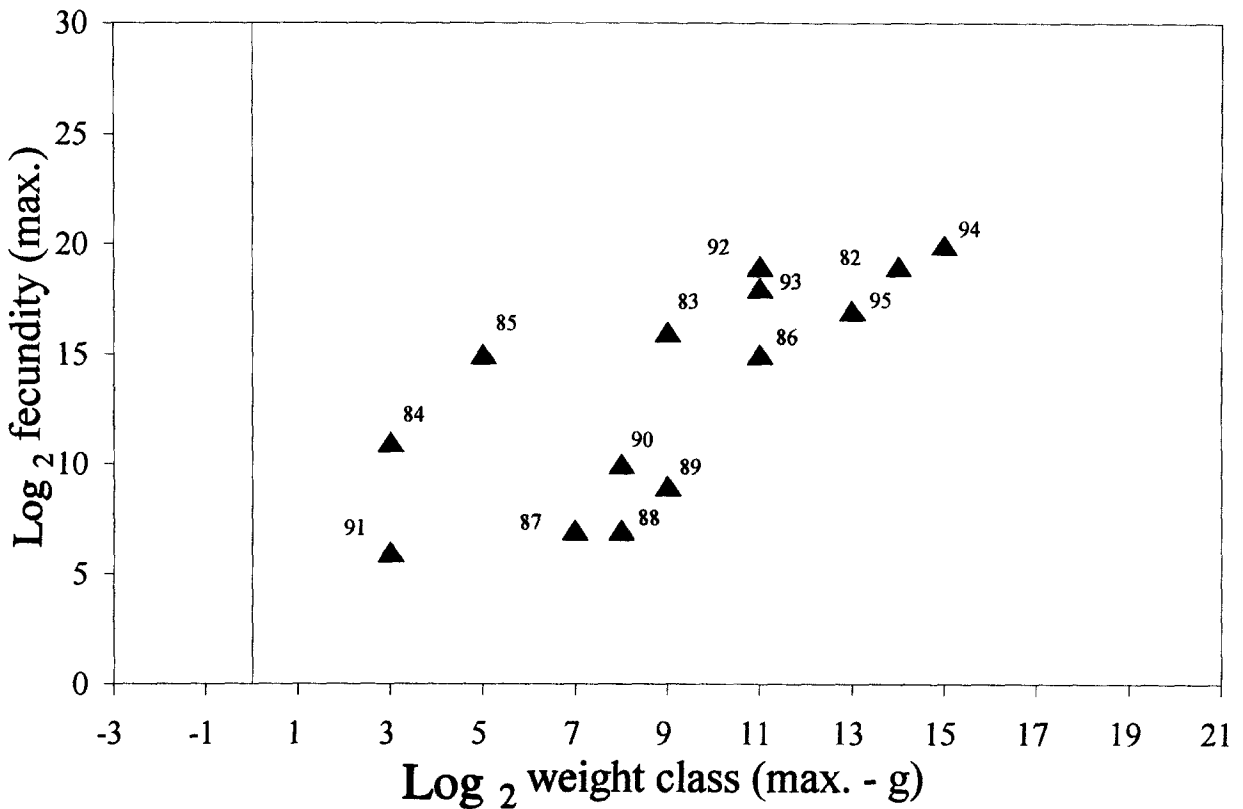


Fig. 12. Relationship between species' maximum fecundity and maximum size among the demersal oceanic representatives of the orders Lophiiformes, Beryciformes, Syngnathiformes, Scorpaeniformes and Pleuronectiformes ($n = 14$) of the North Atlantic Basin (log₂ groupings). (Species are identified by number from Appendix 3b).

ent relationship of known fecundity with size is seen within seven oceanic representatives of the largely benthic family Zoarcidae (Fig. 11, ref. no. 73–81). Little observed difference in fecundity (range 2^4 to 2^6) occurs over some 8 log₂ orders of magnitude in size, while the eighth species, *Lycodes esmarkii* departs somewhat from this trend (2^{10} – ref. no. 76 – Fig. 11). This relatively low fecundity accompanies large egg size (3 mm + diam., Johnsen 1921, Musick et al. 1975, Markle & Wenner 1979, Silverberg et al. 1987). As Mead et al. (1964) pointed out, some form of parental care is implied by this style. Indeed *Melanostigma atlanticum* (ref. no. 80 – Fig. 11), which has taken to a pelagic existence, was postulated to spawn demersally (Markle & Wenner 1979). Recently it was collected from a box-core sample in a sub-surface burrow complete with eggs (Silverberg et al. 1987). The large investment per egg in this group typifies the fundamental patterns of low rela-

tive fecundity correlated with a benthic life-style. This implies direct development associated with a precocial life-history style (Flegler-Balon 1989), exemplifying a 'hole nesting guarder' in Balon's (1990) scheme of reproductive guilds. It is noteworthy that Andriyashev (1953) treated the diverse deep-sea zoarcids as secondarily deep-water forms and pointed out that features of this group are their benthic habit and few eggs spawned on the bottom.

Miscellaneous species. – While fishes from a variety of orders (i.e. 15, 18, 20, 21, 23 – Appendix 2) comprise this group (Fig. 12), the trend among those represented appears to show a roughly linear increase in fecundity with weight, similar to the majority of teleost groups. Noteworthy is *Sebastes norvegicus* (ref. no. 86 – Fig. 12) for its ovoviviparity [an 'obligate lecithotrophic live bearer' in Balon's (1990) classification], with high fecundity on a scale

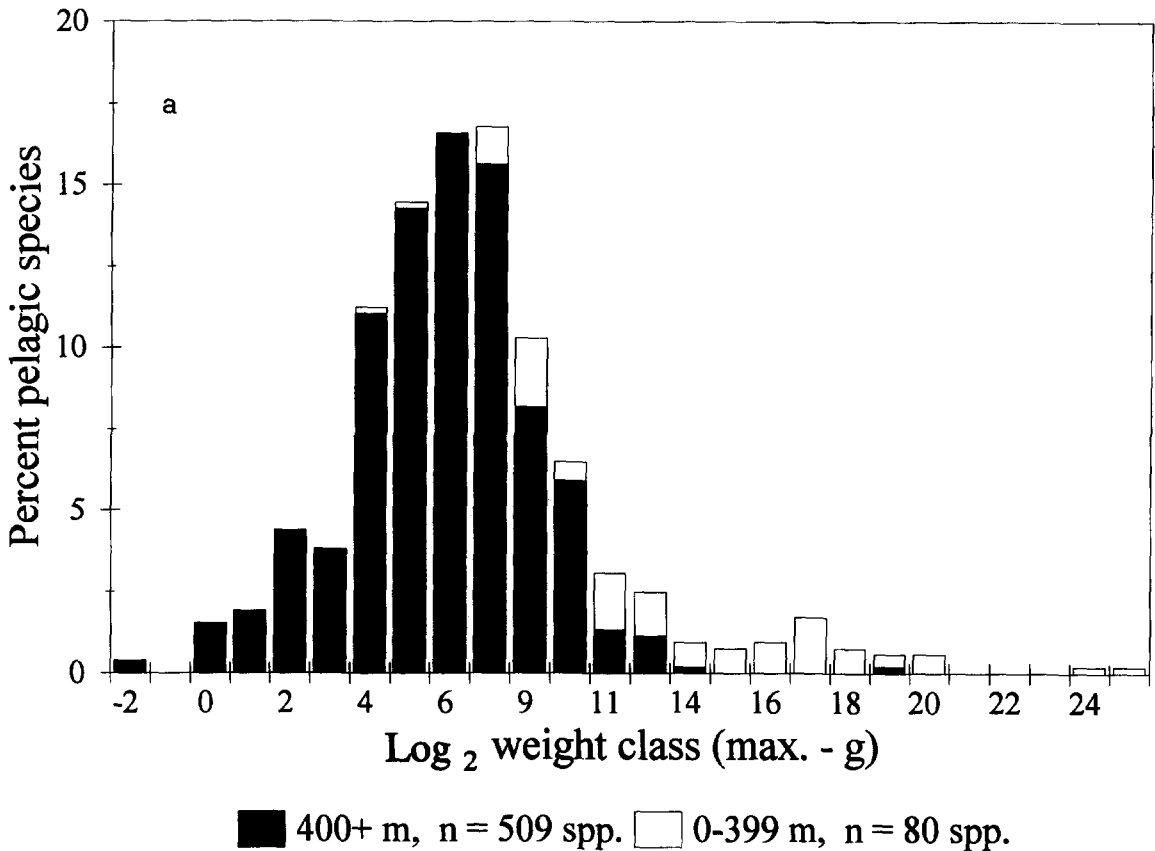


Fig. 13. Overall size spectra based upon maximum known sizes attained by oceanic species of the North Atlantic Basin: a – 589 pelagic species from the upper and lower depth zones, b – 505 demersal species from four depth zones.

equivalent to that of the oviparous bythitoid, *Cataetx laticeps*.

Bathymetric influence on reproductive effort, implied from the overall size spectra of pelagic and demersal fishes in the North Atlantic

Species size spectra indicate responses to evolutionary pressure, while giving some idea of the range of food sources available for exploitation. Haedrich & Merrett (1992) developed this theme, showing that most demersal deep-sea species are foragers/scavengers. They exploit allochthonous food sources from shallower layers, migrating mid-water fauna and, especially among species of small adult size at abyssal depths, small particles within the benthic boundary layer. Haedrich & Merrett

(1992) pointed out that the broader, flatter spectra indicated variation in food sources, while 'spikey' spectra suggested concentration on a certain particle size.

From the point of view of reproductive styles on an ocean basin scale, therefore, an analysis of species size spectra provides an insight to the composition of reproductive contributions among the species of an assemblage, assuming the relationship between body size and fecundity confirmed here. When the size spectra for pelagic and demersal species are plotted as frequency distributions they are found to differ, especially when considered by depth (Fig. 13a, b).

Taken overall, the pelagic size spectrum has an asymmetric distribution, peaking in the weight class range 2^4 to 2^9 g (16 to 511 g maximum size) and with an extended 'tail' to size class 2^{25} g (33.5 to 67.1 t –

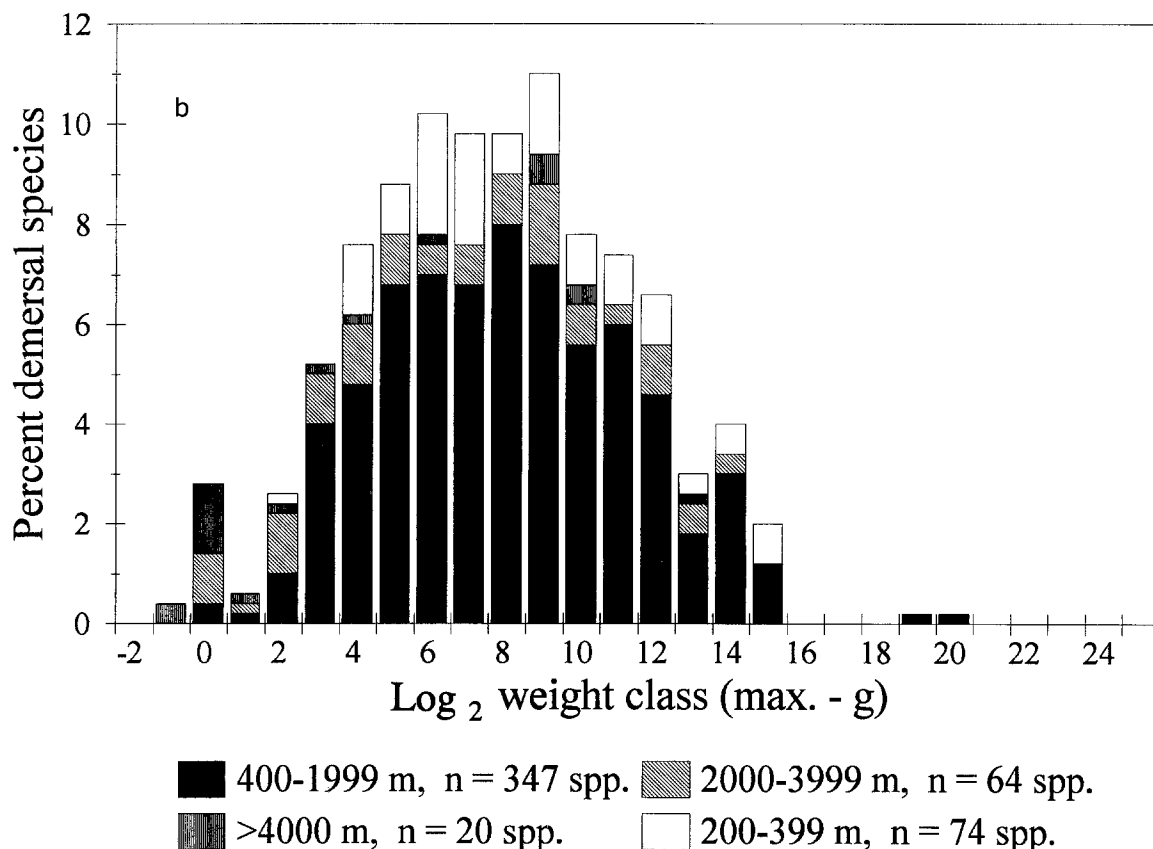


Fig. 13. Continued.

Fig. 13a). The peak of the demersal size spectrum is broader (range 2^4 to 2^{12} g: 16 to 8191 g), without extension into the higher size categories (Fig. 13b). Note, however, that these figures are directly comparable only below the 400 m level (see Materials and methods).

Considered by depth strata, it is evident that those pelagic, secondarily deep water (sensu Andriyashev 1953 – see p. 207), species dwelling in the upper 400 m dominate the larger weight classes (Fig. 13a). (The counterpart to the upper 200 m of this zone in the demersal habitat falls outside the limits of this study. It is unknown whether inclusion of demersal species from the shelf would extend the size spectrum into the larger size classes similarly.) The lower pelagic size spectrum (400 + m) contributes almost entirely to the peak at sizes 2^4 to 2^9 g. [The single representative at 2^{10} g is the swordfish, *Xiphias gladius* (ref. no. 59 – Fig. 6). Recent sonic tag-

ging work has shown that this species, in contrast to other billfish, spends most of its day below 400 m (Block 1991) and is therefore included in the lower zone.] Subdivision of the demersal size spectrum, on the other hand, broadly maintains similar distributions among zones (Fig. 13b). Within this overall distribution, however, there is a perceptible shift in size class dominance between the two shallower strata (larger classes dominating) and the two deeper strata (smaller classes dominating). Most notably, the abyssal species (> 4000 m) dominate the smallest size classes.

While Figure 13 represents the overall situation, do the assemblages found at particular localities follow the same pattern? Spectra constructed from the data given by Merrett et al. (1991a, b) for the Porcupine Seabight/Abyssal Plain (PSB/PAP) assemblage in the eastern North Atlantic, together with that given by Merrett (1987) for the assemblage at

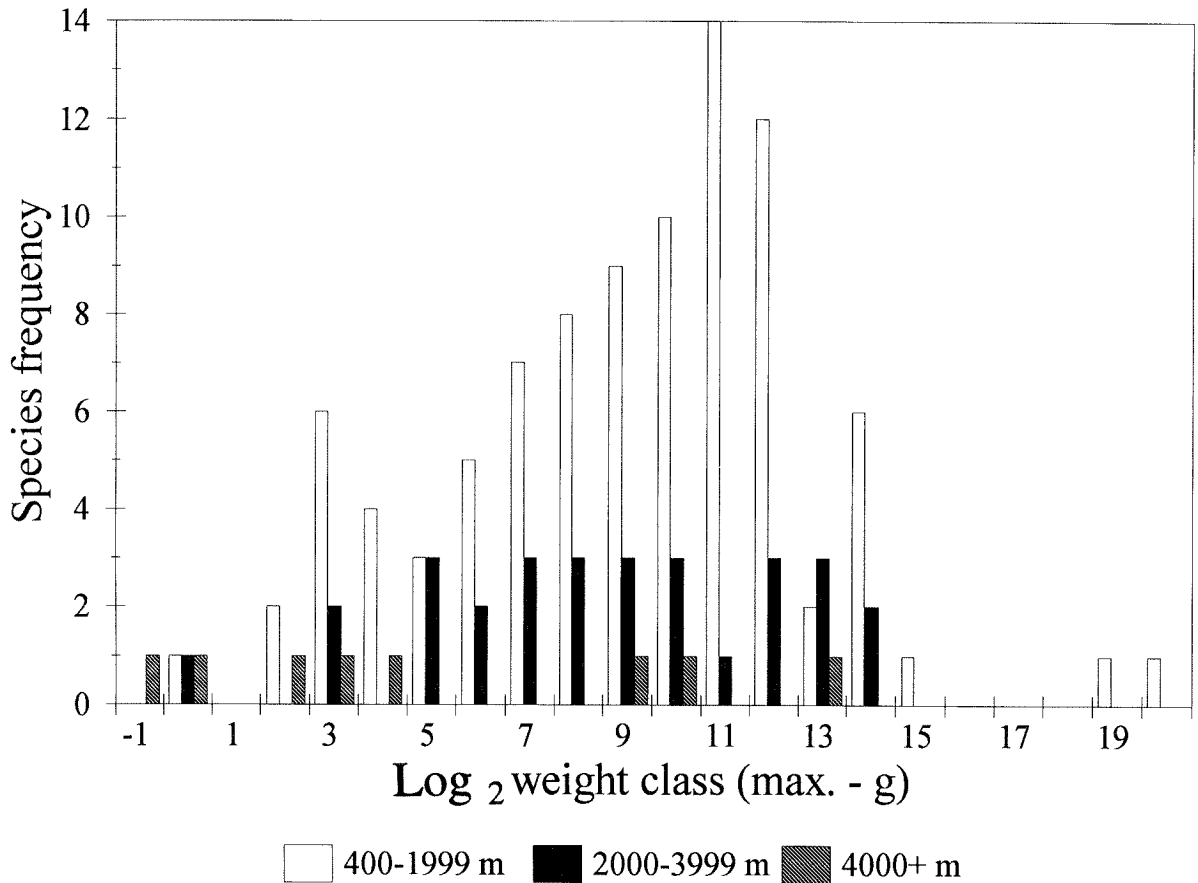


Fig. 14. Size spectra based upon species' adult maximum size of the demersal ichthyofauna sampled from the Porcupine Seabight/Abyssal Plain (PSB/PAP) and the Madeira Abyssal Plain (MAP), eastern North Atlantic, by depth strata (from Merrett 1987, Merrett 1992a, b).

5400 m in the Madeira Abyssal Plain (MAP) and based upon species adult maximum size are given in Figure 14. By implication from the body size-fecundity relationship, the pattern of reproductive effort reflected by species size classes is broadest on the slope. A narrow peak occurs among species of 2^3 to 2^4 g and a much broader one is evident among species of larger adult size which peaks in the 2^{11} to 2^{12} g size classes. At continental rise depths species representation among the largest size classes is curtailed. In the abyss representation is concentrated within the smaller categories (2^{-1} to 2^4 g) and the larger ones (2^9 to 2^{13} g). It is evident that this specific example differs most markedly in species size representation at slope depths in comparison with the basin-wide situation (Fig. 13b). Whatever the cause, the species composition of the size classes, with re-

spect to reproductive style, shows that each class contains a mix of family representation. Such is to be expected with relatively few size classes in relation to the number of species represented. Yet, in general, each family is represented across a wide range of size classes (e.g. the 11 species of macrourid occupying the 400–2000 m depth range occur in the following \log_2 size classes: -2, 3, 6 (2), 7, 8 (2), 9 (2), 10, 11).

To illustrate the complexity of the overall situation, Table 2 indicates the composition of each size class in terms of presumed life-style, reproductive mode and known or presumed fecundity pattern of the major zones, the slope and rise. Relative to the ubiquity of the benthopelagic species among the size classes, benthic species, although sparsely distributed over a wide size range, are most prevalent

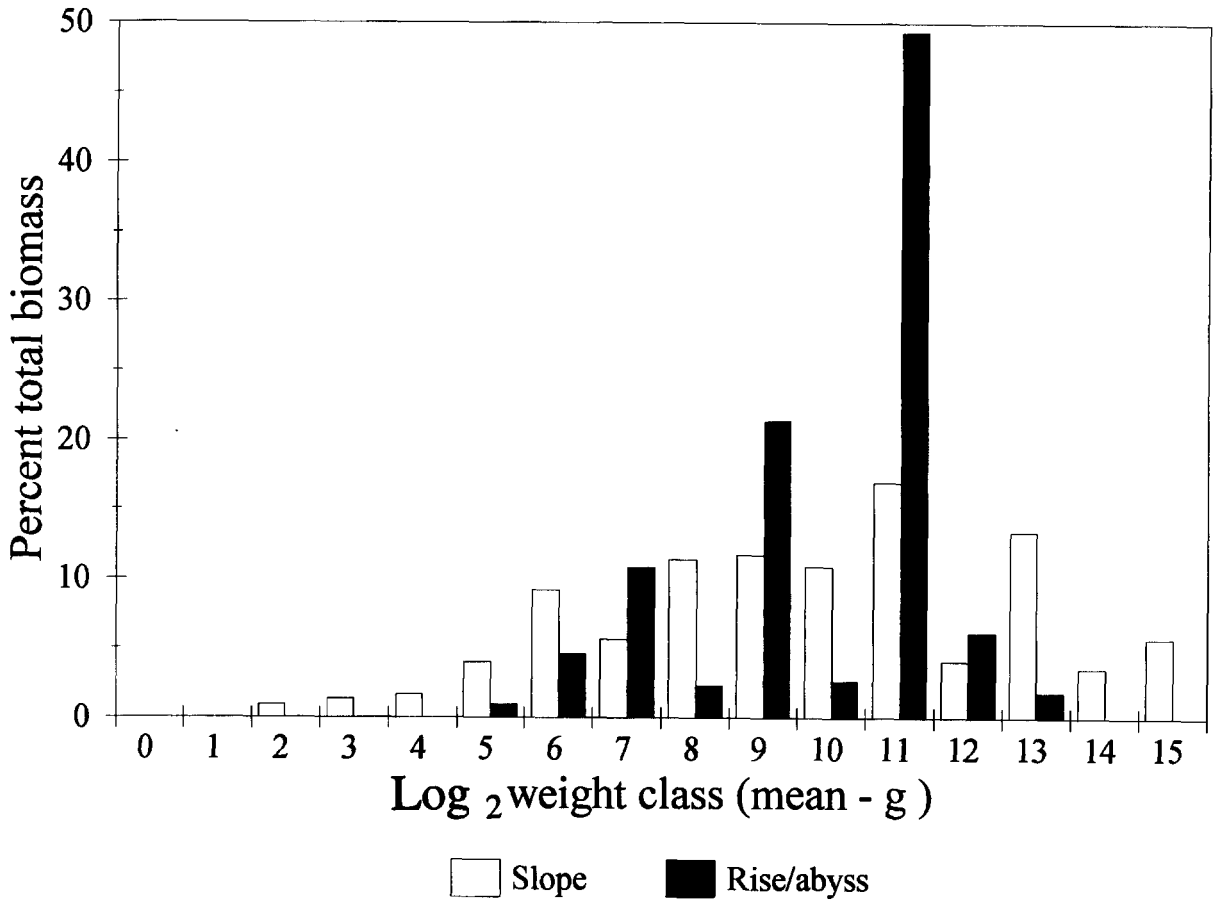


Fig. 15. Biomass spectra for demersal fish sampled from the eastern North Atlantic, from PSB continental slope depths (200–2000 m) and PSP, PAP & MAP continental rise and abyssal depths (2000–5400 m) (after Haedrich & Merrett 1992).

within the 2^7 to 2^{10} g span. Most species are gonochoristic, with only two hermaphroditic species each on the slope and rise. Most species fall into the small egg/high fecundity category and span all but the largest size groups. Species with small eggs and low fecundity are limited to 3 species only (2 benthic) within the size range 2^3 to 2^5 g. Species producing large eggs usually attain large adult size (2^7 to 2^{10} g). Most have relatively low fecundity, but five species with large eggs and medium fecundity occur within the 2^{10} to 2^{13} fecundity range. On the slope, chondrichthyans occupy the largest size classes and the viviparous ones are represented in categories larger than 2^{11} g. Viviparity, small egg/high fecundity and large egg/low or medium fecundity are roughly equal styles among species of adult size of

2^{10} to 2^{24} g. At rise levels evident trends seem similar, apart from the general lack of chondrichthyans (2 rays only).

Using biomass spectra from known populations of pelagic and demersal fishes, what reproductive arrangements appear to dominate on a basin-wide scale?

Species size spectra indicate the allocation of potential reproductive effort across the spectrum of diversity for the overall fish assemblage. They do not take the relative abundance of the constituent species into account, however, and therefore shed no light on the total assemblage effort realized. Bio-

mass spectra provide the frequency distribution of individuals by weight within each size class represented in the assemblage (Gaedke 1992). Such an approach includes all individuals of the assemblage, of course, both pre-reproductive and reproductive. Nevertheless, in this preliminary investigation, it is a useful comparative indicator of any regional or bathymetric variation in the distribution of energy flow (see Gaedke 1992) and reproductive effort on a basin-wide scale. In broad terms, the shape of the biomass spectrum reflects the section of the species size spectrum potentially contributing the most to the total fecundity of the assemblage overall.

Quantifying such an estimate for an entire ocean basin is far beyond the scope of the information currently available. Well-sampled populations do provide information on biogeographic and bathymetric variation. In general, inferences on reproductive style can be drawn from the overall shape of biomass spectra. Those that have been called 'flat' (Sheldon et al. 1977) suggest a wide range of reproductive arrangements across the altricial and precocial interspecific range. Spectra that have been called 'spikey' (Sprules & Knoechel 1984, Haedrich 1986) imply a concentration of potential reproductive effort over a narrow range of size classes. Thus, spectra which are spikey in the smaller size classes suggest a preponderance of species which probably incline towards altricial life-history traits and reproductive arrangements (Adams 1980, and see p. 208). Spikey spectra in the larger size classes probably indicate a more precocial pattern.

Biomass spectra were also constructed for the deep demersal fishes of the PSB/PAP/MAP area (Haedrich & Merrett 1992). Such similarity was found among the patterns displayed among the chosen strata both at slope and at rise to abyssal depths that the information was combined (200–2000 m and 2000–5400 m, here Fig. 15). The biomass spectrum for slope depths can be termed flat, which indicates that potential reproductive effort is relatively evenly spread across the spectrum of individual fish sizes and, by analogy, species diversity. Deeper, on the continental rise and abyss, however, the biomass spectrum is spikey with a very distinct mode at size 2^{11} g (2 kg). Thus at these levels there is

a favoured reproductive unit size whose effort is channelled through relatively high fecundity.

Similar data are available from one pelagic study, that of Haedrich (1986), which provides an insight to the changing shape of biomass spectra on a regional scale. Haedrich found that, among the meso-pelagic fish assemblage of the North Atlantic Basin, biomass spectra of very different patterns occurred in different regions (Fig. 16). A very spikey distribution occurred in the sub-Arctic, with by far the most biomass concentrated in the 2^{-1} g (0.5 to 0.9 g) size class (Fig. 16a). Conversely, both the northern and southern Sargasso data produced a flat biomass spectrum, with biomass distributed much more evenly over the total size range of fishes (Fig. 16b). The Azores-Britain and, to some degree, the Guinean regions were found to be intermediate between these two extremes (Fig. 16a). The implications here are that reproductive effort in the sub-Arctic region is concentrated among (few) species of small adult size. The emphasis of one size class is reduced in the other areas, broadening the size class (and therefore fecundity) allocation to reproductive effort.

Reproductive style and food availability

While potential ichthyofaunal fecundity levels can be associated with various oceanic zones of productivity as above, teleost conformity to the idealized concepts of an altricial and precocial range (the 'al-prehost' concept of Balon 1990) means that variations in reproductive style within major taxa are similarly associated with such zones.

Pelagic

The exponential decline of biomass with depth in midwaters (Angel & Baker 1982) limits that majority of pelagic fishes which tend towards the precocial end of the range to the upper zone (e.g. scombroid fishes and pelagic sharks). Both examples are top predators, but display very different reproductive patterns which reflect phylogenetic origins and constraints. Scombroids are highly fecund and subject to high juvenile mortality. They exploit all size classes of food supply during their life history. Pe-

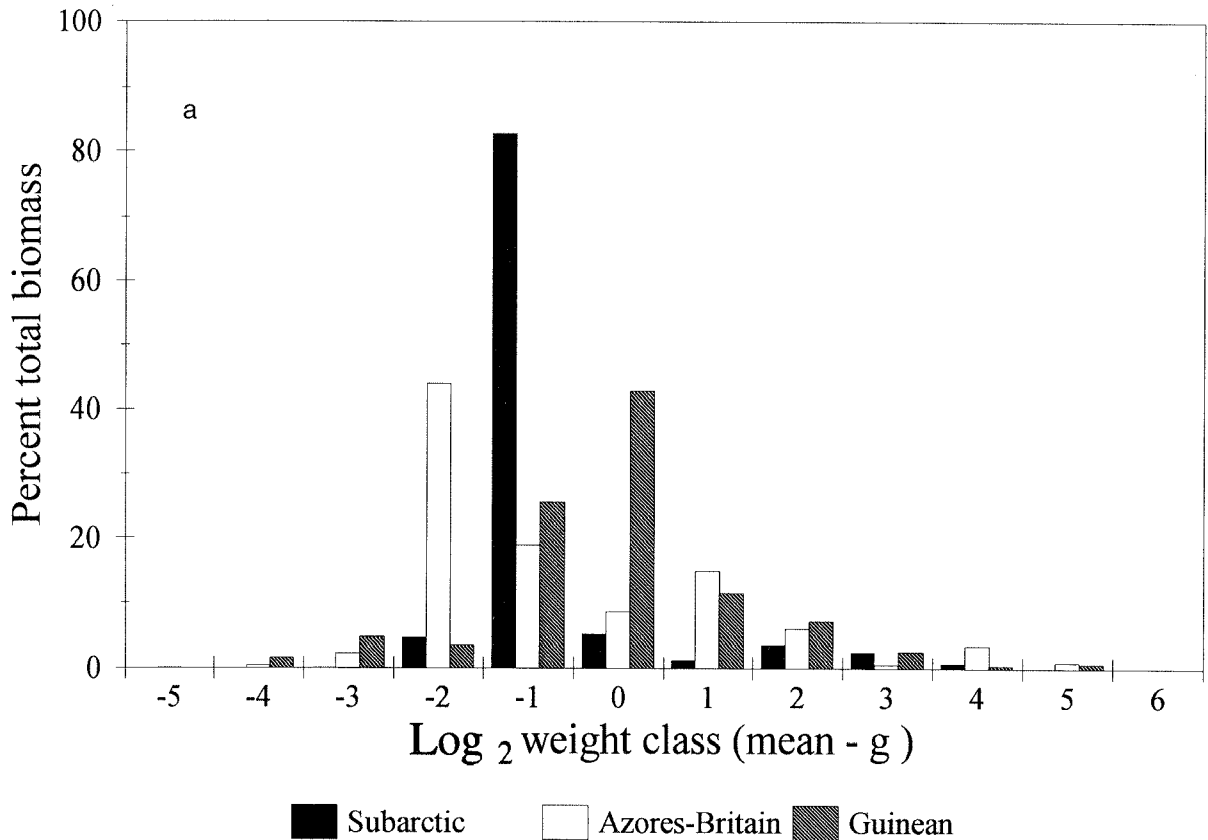


Fig. 16. Biomass spectra for oceanic mesopelagic fishes sampled in the North Atlantic: a – Atlantic sub-Arctic, Azores-Britain and Guinean regions; b – northern and southern Sargasso Sea regions (after Haedrich 1986 and personal communication).

lagic sharks, on the other hand, are viviparous with a relatively low fecundity resulting in a style which by-passes juvenile mortality and a dependence on small size classes of food. The large young are produced directly into the top predator feeding category.

Those fish that occur deeper in midwaters, however, attain considerably smaller adult size relative to their shallower-living counterparts (cf. Fig. 13a). The midwaters, in daytime between depths of ca. 400 m from the surface to 100 m off the sea-bed, are the headquarters of the so-called 'Lilliputian fauna' of the deep-sea (Murray & Hjort 1912).

The vertical effect on food availability results in an overall shift among species towards the altricial end of the range. A variety of reproductive styles are employed among this ichthyofaunal assemblage where resources are limited. Here species exploit-

ing the lower trophic levels are both more numerous in the fauna and individually most abundant. They are typically of very small adult size and short lifespan (e.g. sternoptychids – Howell & Krueger 1987; *Cyclothone* – Badcock & Merrett 1976, Marshall 1984, Miya & Nemoto 1986a, b, 1987a, b, 1991, McKelvie 1989; myctophids – Kawaguchi & Mauchline 1982, Oven 1985, Karnella 1987, Albikowskaya 1988; melamphoids – Keene et al. 1987) and constrained by their body size to low fecundity. Only among predators higher up the food chain does body size allow for higher fecundity. Even so, it is probably trophic limitation on the largely bathypelagic ceratioid angler species, which causes some at least to become demersal at fully adult size (e.g. *Thaumatichthys* – Bertelsen & Struhsaker 1977, *Gigantactis* – personal observation).

Childress et al. (1980) demonstrated contrasting

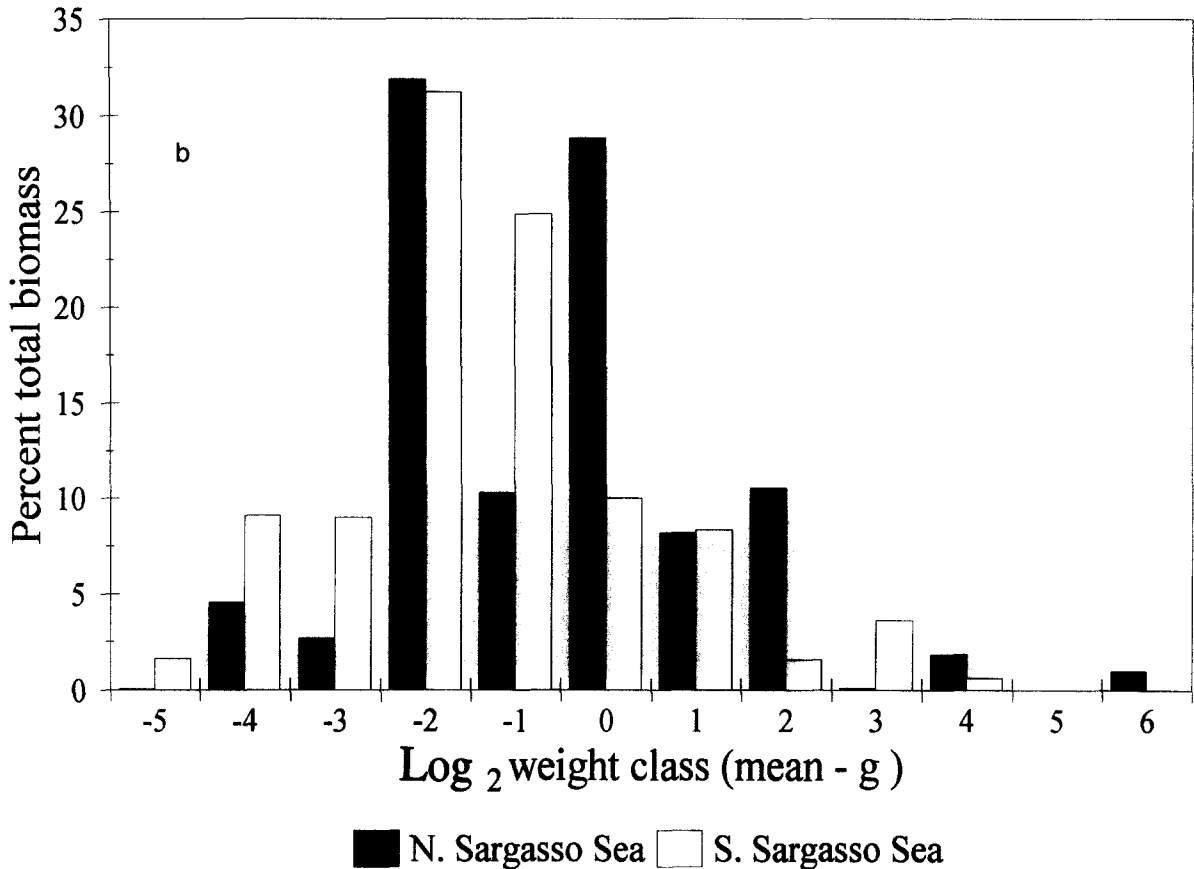


Fig. 16. Continued.

patterns in growth, energy utilization and reproduction among epi-, meso- and bathypelagic fishes in waters off southern California. They found that epipelagic (*sensu stricto*) fishes were adapted to large size, rapid growth, long life and early, repeated reproduction. Mesopelagic fishes shared the long life and early, repeated reproduction, but were characterized by small size and slow growth. Bathypelagic fishes, on the other hand, generally showed large size and rapid growth which was achieved by high relative growth efficiencies facilitated by low metabolic rates. They also had somewhat shorter lives and late reproduction (perhaps semelparity). (While the area illustrated is in a possibly atypical part of the Pacific Ocean, these results are noteworthy).

In contrast to the mesopelagic species studied by Childress et al. (1980) which were all diurnal migrants, Marshall (1984) discussed the evident pae-

domorphic trend in the non-migrant, mesopelagic *Cyclothone*. Paedomorphism, he argued, might result from competition with migrating species, which dominate the fauna and are annual fishes in the tropics (Childress et al. 1980). According to Marshall (1984), as non-migrants these *Cyclothone* have access to a lesser food supply for growth and development than do migrant species. Thus neoteny might offer them the only opportunity to mature in one year, competitively with migrant species exploiting the richer surface waters. In agreement with the trend found by Childress et al. (1980) among (non-migrant) bathypelagic fishes, Marshall (1984) pointed out that bathypelagic *Cyclothone* species are both larger in adult size and have greater fecundity than their mesopelagic congeners. In addition, using the North Atlantic data of Badcock & Merrett (1976), he showed that the abundance of bathypelagic *C. microdon* was approximately half

that of mesopelagic *C. braueri*. While bathypelagic fish species may demonstrate the life-history characteristics observed by Childress et al. (1980), reduced standing stocks of fish (i.e. biomass) in this zone are consistent with the vertical decline in food availability (sensu Angel & Baker 1982, see above). This reduction in fish biomass, and therefore abundance, with depth is a general trend. With egg production ultimately dependent on species adult size and abundance, the implication is that overall egg production from pelagic spawning teleosts at mesopelagic and bathypelagic levels may approach parity.

Towards the surface, the productive euphotic layers sustain the maximum pelagic biomass. In tropical and temperate regions, at least, this biomass is distributed rather evenly among all size classes. Top predator teleosts are in relatively low abundance (e.g. istiophorids) but with commensurately high fecundity. Thus overall egg production among the varying size classes of pelagic oceanic teleosts may be of the same order of magnitude, considering the scaling of fecundity with body size in conjunction with the hypothesis developed by Sheldon et al. (1972) and others that roughly equal concentrations of material occur at all particle sizes from bacteria to whales.

Demersal

The seabed acts as the ultimate sink for oceanic production. Food particles of all sizes sink and accumulate there. This offers the diverse ichthyofauna far greater food supplies than are encountered in the overlying midwaters. Ichthyofaunal demersal biomass, abundance and mean fish size decrease with increased soundings from a peak at mid-slope depths (Merrett et al. 1991b). Only in deep mid-ocean basins beneath oligotrophic surface waters, however, is the size spectrum dominated by species of very small adult size (2^0 g – Figs 14 and 13b).

Food supplies are sufficient for some top predators to extend to abyssal levels. In contrast with the pelagic realm, large demersal elasmobranchs (e.g. rajids and squalids) are distributed down to 3000 m or so. While the rajids are oviparous and of unknown fecundity, squalids have the potential to bear up to about 30 well-developed young (Fig. 7)

into the top predator trophic level down to these depths. Typically teleost fecundity is high, with the implication that the small eggs develop pelagically through larval stages, the indirect or transitory ontogeny of the altricial life-history style (Flegler-Ballon 1989). This is exemplified by the synaphobranchid, halosaur and notacanth (Fig. 8), ipnoid (Fig. 9), gadiform (Fig. 10) and ophidiid [*Dicrolene* (ref. no. 68 – Fig. 11) and *Spectrunculus* (ref. no. 69 – Fig. 11)] fecundity patterns. The alepocephalids, however, have a more precocial style with generally much larger eggs (e.g. Golovan & Pakhorukov 1984, Crabtree & Sulak 1986), with implied demersal development (Fig. 9). It should be noted, however, that midwater members of this family also have large eggs – e.g. *Bathylaco* (ref. no. 45 – Fig. 9) (Nielsen & Larsen 1968, Nielsen 1972). Moreover, at least one mid-water species (*Xenodermichthys copei*, ref. no. 42 – Fig. 9) has been suggested to descend to the bottom to spawn (Markle & Wenner 1979.) Among the viviparous bythitoids, the aphyonids have low clutch sizes and advanced young (Nielsen 1969), while the bythitid, *Cataetx laticeps* (ref. no. 70 – Fig. 11), has a fecundity comparable to that of oviparous ophidioids, but releases free embryos. Zoarcids display a precocial pattern with fecundities which seem to mirror those of the squalid sharks, in that egg number seems relatively uncorrelated with species adult size (Fig. 11). Since one species, at least, is known to reproduce in burrows [*Melanostigma atlanticum* (ref. no. 80 – Fig. 11) – Silverberg et al. 1987 and see Kendall et al. 1983], this may be a trend among other deep living members of this family (M.E. Anderson personal communication). The protection thus afforded would allow for greater energetic investment in a few large eggs for release into the environment as advanced offspring.

Conclusion

The pelagic oceanic fauna clearly separates into two phylogenetic groupings. The surface waters, down to about 400 m, contain one group representing 'more advanced' orders consistent with the neritic ichthyofauna. Below this layer resides the true

deep-sea ichthyofauna composed of representatives of generally 'less advanced' orders. The ordinal representation by species is, again, strikingly different between the pelagic and demersal assemblages. Changes occur also within the demersal ichthyofauna alone. They indicate, for instance, that chondrichthyans are important constituents to little deeper than slope waters, while the salmoniforms, aulopiforms and ophidioids characterize the rise and abyssal assemblages.

Close to the surface and to the sea-bed, where the environment is relatively rich in food, a wide range of fish sizes (by species) may co-occur to exploit a wide range of relatively easily accessible and abundant particle sizes. Abundant, diminutive species, which are planktivorous throughout their life history, can compete successfully with large teleosts which soon pass through a planktivorous state as young and grow to become top predators. Adult large teleosts also compete with sharks whose young never compete for particles of small size, but are born directly into the top predator trophic level. Indeed, the advanced modes of viviparity developed by the oceanic lamniform and carcharhiniform sharks of the North Atlantic maximize the size at which the young are born and hence the advantage the young have relative to other organisms in the oceanic food web (Compagno 1990). In the midwaters, where the depth dimension strongly influences food availability, the pelagic ecosystem declines in species richness and biomass to minimal levels around 3000 m. Only particles of a relatively small size and size range may be sufficiently concentrated to sustain a relatively sparse ichthyofauna in which large top predators are (energetically) denied a living. In the shallower parts of this region, therefore, the prevalent pattern is obligatorily modest fecundity constrained by small body size, but substantially compensated for by a high abundance (if not density). Yet reproductive adaptations displayed by a particular taxon (body size/egg size/fecundity balance, in this case) are often a closer reflection of the evolutionary history of that group than of selection pressures in the contemporary context (Crabtree & Sulak 1986). Hence, while such parameters as those above, together with species abundance and generation time, may have long-

standing phylogenetic origins, many arrangements for maximizing fecundity and survival (e.g. sexual dimorphism, synchrony in hermaphroditism, teleost viviparity, 'batch' spawning, seasonal synchrony, egg rafts, parental care, etc.) may be associated with more contemporary selection pressures and provide trade-off and alternative life history opportunities.

The current review indicates a variety of reproductive trends at ordinal or lower systematic levels within the North Atlantic Basin. Among the chondrichthyans, the successful deepsea forms utilize 'extended oviparity' (Scyliorhiniformes, Rajiformes and Chimaeriformes) or 'yolk-sac viviparity' (Hexanchiformes, Squaliformes), while the 'viviparous cannibalism' of the Lamniformes dominates in the food-rich near-surface waters.

Altricial non-guarding egg scatterers (*sensu* Ballon 1990) are the norm among the teleosts. The Anguilliformes are characterized by considerable sexually dimorphic changes with increased ripeness, in pelagic forms at least, and semelparity over a probably extended life-span in most species. They and the Notacanthiformes share leptocephalous larvae. The latter group, however, appears to be iteroparous. In contrast to the high fecundity and small egg size displayed by these orders, the Salmoniformes are characterized by low to medium fecundity and large egg size, typical of a more precocial style. 'Batch' spawning is usual in both pelagic and demersal salmoniforms, but the whereabouts of spawning is unknown. The Aulopiformes considered here are synchronous hermaphrodites, a style which may compensate for the reduction in sexual encounters resulting from their benthic life-style. Most are rather small fishes, with low fecundity and small, 'batch'-spawned, pelagic eggs.

The vast majority of the representatives of the orders Stomiiformes and Myctophiformes are pelagic and dominate this assemblage in species richness and abundance. Both orders are composed of altricial, short-lived species of small adult size, with low fecundity and small egg size. Many myctophiforms are nocturnal vertical migrants and exploit the near-surface waters, to facilitate completion of the life-cycle in one year in many species. Sexual dimorphism is expressed by size, sex ratio and photophore

distribution. Many stomiiforms are also nocturnal migrants. The reproductive arrangements of the highly abundant non-migrant species are best known and in this respect are found to be more versatile than are the myctophiforms. For instance, the species of the genus *Cyclothone*, together with others, may display paedomorphic tendencies, protandric hermaphroditism and sexual dimorphism in size, sex ratio and olfactory development. Stomiiforms are also short-lived, 'batch' or 'all-at-once' spawners.

The order Gadiformes is represented by dominant families in the deep demersal ichthyofaunal assemblage, the Macrouridae and Moridae. Reproductively these are altricial generalists of medium to large adult size, with high fecundity and usually small eggs. The majority of species are iteroparous, but possibly at least one of the continental rise/abyssal species may be semelparous, despite its large size and likely longevity. The males in several species are macrosomatic. Females may be 'all-at-once' or 'batch'-spawners.

The Ophidiiformes are largely demersal in the deep-sea. They are composed of one sub-order of oviparous species, the Ophidioidei, and another of ovoviviparous species, the Bythitoidei. Ophidioid species occupy a wide range of size classes but are generally altricial, displaying high fecundity and small egg size. The bythitoid species also cover a wide size range with precocial reproductive styles involving direct development, which span small neotenic species bearing few advanced young (family Aphyonidae; benthopelagic and demersal), to much larger species which produce great numbers of free embryos (Bythitidae). (This latter adaptation is one shared with some species of the order Scorpaeniformes). Sexual dimorphism in the Bythitoidei is expressed in the intromittent organ of males. The spermatophores produced by males are believed to function in a storage capacity in impregnated females.

Deep-sea Lophiiformes are mostly bathypelagic lie-and-wait predators of the sub-order Ceratioidei. They have exploited extremes of sexual dimorphism in size, culminating in male parasitism in some families. Species of this order are oviparous and display high fecundity and small egg size. In

common with certain shallow lophiiform representatives, at least one species of ceratioid protects its egg mass in a mucus veil.

Deep-sea members of the order Perciformes are dominated in the North Atlantic by the sub-order Zoarcoidei. Most speciose is the benthic family Zoarcidae, which are oviparous and of moderate size. Their precocial lifestyle, with low fecundity and large eggs, is contrary to oceanic teleost trends. Some evidence suggests that burial of eggs occurs for protection, which could be expected to enhance the survival rate. The Parabrotulidae are diminutive pelagic ovoviviparous zoarcoids that produce few advanced young.

Finally, this review of deep-sea fish reproduction since the work of Mead et al. (1964), coupled with an endeavour to describe ichthyofaunal organization on an ocean basin scale via a variety of parameters associated with reproduction, has highlighted the extent of the basic information still outstanding. Further wide-ranging input (data on early ontogenetic structures; species size data; accurate, size-related, distributional data; patterns of oogenesis in the majority of species, etc.) is now necessary before the web of possible correlations advanced here can be clarified.

Acknowledgements

I dedicate this paper, in particular, to the fond memory of ET (Ethelwynn Trewavas) in recognition of her outstanding contributions and lifelong devotion to ichthyology. Certain weight-length data were generously provided by R. Froese (ICLARM), J.D.M. Gordon (SAMS), R.L. Haedrich (Memorial University, Newfoundland – WHOI data), A. Post and Christine Karrer (ISH). I am very grateful to them and to the many people with whom I have had discussions on all aspects of this work. R.H. Beverton was especially helpful in the early stages of the paper and R.L. Haedrich, N.B. Marshall, J. Nielsen (Zoological Museum, Copenhagen), and J.R. Paxton (Australian Museum) put much effort into improving the final draft of the manuscript. I thank them all particularly.

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Appendix I. Log₂ (maximum) weight class frequency distribution of pelagic oceanic species among the orders (numbered arbitrarily from less to more advanced) represented in the North Atlantic Basin: a - 0-399 m, b - 400 + m.

Ord. no.	Orders	Log ₂ weight class																																											
		-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25																
a PELAGIC - 0-399 m.																																													
1	Myxiniformes																																												
2	Hexanchiformes																																												
3	Squaliformes																																												
4	Lamniformes											1									8	3	1				1	1																	
5	Rajiformes											1																																	
6	Chimaeriformes																																												
7	Anguilliformes																																												
8	Notacanthiformes																																												
9	Salmoniformes																																												
10	Stomiiformes																																												
11	Aulopiformes																																												
12	Myctophiformes																																												
13	Gadiformes											1																																	
14	Ophidiiformes													1																															
15	Lophiiformes											1																																	
16	Cyprinodontiformes			1						5		6		1																															
17	Lampriformes											1		2		1		1		1				2																					
18	Beryciformes																																												
19	Zeiformes																																												
20	Syngnathiformes																																												
21	Scorpaeniformes																																												
22	Perciformes			1		4		1		4		2		5		1		4		3		3		3		1		1		1															
23	Pleuronectiformes																																												
24	Tetraodontiformes											1				1		1				1		2																					
25	Dactylopteriformes																																												
b PELAGIC - 400+ m.																																													
1	Myxiniformes																																												
2	Hexanchiformes																																												
3	Squaliformes											1		1		1																													
4	Lamniformes																																												
5	Rajiformes																																												
6	Chimaeriformes																																												
7	Anguilliformes			1		3		1		3		5		1		3		2																											
8	Notacanthiformes																																												
9	Salmoniformes							15		18		8		7		6																													
10	Stomiiformes	2		3		7		5		4		13		21		23		33		26		5		8		1																			
11	Aulopiformes					6		1		4		11		13		3		1		1		1		1																					
12	Myctophiformes	1		1		4		9		14		16		21		15		6																											
13	Gadiformes					1		1				1				1		1																											
14	Ophidiiformes	2																																											
15	Lophiiformes			1						6		11		13		24		14		3				1																					
16	Cyprinodontiformes																																												
17	Lampriformes			1		1		1				1																																	
18	Beryciformes			4		2		4		1		5		8		3		4		2																									
19	Zeiformes																																												
20	Syngnathiformes																																												
21	Scorpaeniformes			1																																									
22	Perciformes	2						2		8		2		2		4		3				1		5		1				1															
23	Pleuronectiformes																																												
24	Tetraodontiformes																																												
25	Dactylopteriformes																																												

Ord. no.	Orders	Log-2 weight class																																		
		-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25							
c DEMERSAL - 2000-3999 m																																				
1	Myxiniformes																																			
2	Hexanchiformes																																			
3	Squaliformes																																			
4	Lamniformes																																			
5	Rajiformes											1											1													
6	Chimaeriformes																																			
7	Anguilliformes											1											1													
8	Notacanthiformes											1	1																							
9	Salmoniformes											1	2	1											1	1	1									
10	Stomiiformes																																			
11	Aulopiformes											2	1	1											1											
12	Myctophiformes																																			
13	Gadiformes											1											1	2	3											
14	Ophidiiformes											5											6	2	1	2	1	3	2	1	1					1
15	Lophiiformes																					1														
16	Cyprinodontiformes																																			
17	Lampriformes																																			
18	Beryciformes											1																								
19	Zeiformes																																			
20	Syngnathiformes																																			
21	Scorpaeniformes											6	2	1																						
22	Perciformes																					1	1	1												
23	Pleuronectiformes																																			
24	Tetraodontiformes																																			
25	Dactylopteriformes																																			

d DEMERSAL - 4000+ m																																					
1	Myxiniformes																																				
2	Hexanchiformes																																				
3	Squaliformes																																				
4	Lamniformes																																				
5	Rajiformes																																				
6	Chimaeriformes																																				
7	Anguilliformes																																				
8	Notacanthiformes																																				
9	Salmoniformes																					1															
10	Stomiiformes																																				
11	Aulopiformes	2	1											1																							
12	Myctophiformes																																				
13	Gadiformes																					1											1				
14	Ophidiiformes											5	1	1											2	1											
15	Lophiiformes																																				
16	Cyprinodontiformes																																				
17	Lampriformes																																				
18	Beryciformes											1	1																								
19	Zeiformes																																				
20	Syngnathiformes																																				
21	Scorpaeniformes																																				
22	Perciformes																					1															
23	Pleuronectiformes																																				
24	Tetraodontiformes																																				
25	Dactylopteriformes																																				

Appendix 3. Key to species' representation in the fecundity per weight plots of a – the pelagic species in Fig. 3–6 and b – the demersal species in Fig. 7–12.

	Species	Ref. No.	Species	Ref. No.	
a					
Figure 3			Figure 6		
Lamniiformes	<i>Carcharodon carcharias</i>	1	Anguilliformes	<i>Eurypharynx pelecanooides</i>	43
	<i>Isurus oxyrinchus</i>	2		<i>Monognathus taaningi</i>	44
	<i>Isurus paucus</i>	3	Salmoniformes	<i>Bathylaco nigricans</i>	45
	<i>Carcharhinus falciformis</i>	4		Gadiformes	<i>Micromesistius poutassou</i>
	<i>Carcharhinus longimanus</i>	5	Lophiiformes	<i>Ceratias holboelli</i>	47
	<i>Carcharhinus obscurus</i>	6		<i>Haplophryne mollis</i>	48
	<i>Carcharhinus signatus</i>	7	Cyprinodontiformes	<i>Hirundichthys</i> sp.	49
	<i>Pseudocarcharias kamoharai</i>	8		Perciformes	<i>Coryphaena hippurus</i>
	<i>Prionace glauca</i>	9	<i>Parabrotula plagiophthalma</i>		51
	<i>Alopias superciliosus</i>	10	<i>Katsuwonus pelamis</i>		52
	<i>Sphyrna leweni</i>	11	<i>Thunnus alalunga</i>		53
	<i>Sphyrna mokharran</i>	12	<i>Thunnus albacares</i>		54
Squaliformes	<i>Isistius brasiliensis</i>	13	<i>Thunnus obesus</i>		55
	<i>Squaliolus laticaudus</i>	14	<i>Thunnus thynnus</i>	56	
Figure 4			<i>Istiophorus albicans</i>	57	
Stomiiformes	<i>Cyclothone alba</i>	15	<i>Tetrapterus albidus</i>	58	
	<i>Cyclothone braueri</i>	16	<i>Xiphias gladius</i>	59	
	<i>Cyclothone microdon</i>	17	Tetraodontiformes	<i>Mola mola</i>	60
	<i>Cyclothone pallida</i>	18			
	<i>Cyclothone pseudopallida</i>	19			
	<i>Maurolicus muelleri</i>	20			
	<i>Valenciennellus tripunctulatus</i>	21			
	<i>Vinciguerria attenuata</i>	22			
	<i>Vinciguerria poweriae</i>	23			
	<i>Argyropelecus hemigymnus</i>	24			
	<i>Idiacanthus fasciola</i>	25			
Figure 5					
Myctophiformes	<i>Protomyctophum arcticum</i>	26			
	<i>Symbolophorus rufinus</i>	27			
	<i>Hygophum benoiti</i>	28			
	<i>Lampanyctus macdonaldi</i>	29			
	<i>Lampanyctus alatus</i>	30			
	<i>Lobianchia dofleini</i>	31			
	<i>Myctophum affine</i>	32			
	<i>Myctophum asperum</i>	33			
	<i>Myctophum nitidulum</i>	34			
	<i>Myctophum punctatum</i>	35			
	<i>Notolychnus valdivae</i>	36			
	<i>Notoscopelus krøyeri</i>	37			
	<i>Notoscopelus resplendens</i>	38			
	<i>Benthoosema glaciale</i>	39			
	<i>Ceratoscopelus maderensis</i>	40			
	<i>Diaphus garmani</i>	41			
	<i>Diaphus rafinesquei</i>	42			

	Species	Ref. No.	Species	Ref. No.				
b								
Figure 7								
Hexanchiformes	<i>Hexanchus griseus</i>	1	Figure 10 Gadiformes	<i>Caelorinchus labiatus</i>	50			
	<i>Hexanchus vitulus</i>	2		<i>Coryphaenoides (Chalinura) mediterraneus</i>	51			
	<i>Clamydoselachus anguineus</i>	4		(C) <i>Coryphaenoides guentheri</i>	52			
Lamniformes	<i>Pseudotriakis microdon</i>	5		(C) <i>Coryphaenoides rupestris</i>	53			
				(C) <i>Lionurus carapinus</i>	54			
Squaliformes	<i>Oxynotus centrina</i>	6		(C) <i>Nematonurus armatus</i>	55			
	<i>Centrophorus granulosus</i>	7		<i>Echinomacurus mollis</i>	56			
	<i>Centrophorus lusitanicus</i>	8		<i>Gadomus longifilis</i>	57			
	<i>Centrophorus squamosus</i>	9		<i>Macrourus berglax</i>	58			
	<i>Centrophorus uyato</i>	10		<i>Nezumia aequalis</i>	59			
	<i>Centroscyrmus coelelepis</i>	11		<i>Trachyrincus murrayi</i>	60			
	<i>Centroscyrmus owstoni</i>	12		<i>Trachyrincus scabrus</i>	61			
	<i>Dalatias licha</i>	13		<i>Merluccius merluccius</i>	62			
	<i>Echinorhinus brucus</i>	14		<i>Molva dypterygia</i>	63			
	<i>Etmopterus spinax</i>	15		<i>Phycis chesteri</i>	64			
	Figure 8							
	Anguilliformes	<i>Histiobranchus bathybius</i>	16	Figure 11 Ophidiiformes	<i>Dicrolene intronigra</i>	68		
<i>Ilyophis brunneus</i>		17	<i>Spectrunculus grandis</i>		69			
<i>Synphobranchus kaupi</i>		18	<i>Cataetx laticeps</i>		70			
Notacanthiformes	<i>Aldrovandia affinis</i>	19	<i>Barathronus bicolor</i>		71			
	<i>Aldrovandia phalacra</i>	20	<i>Nybelinella erikssoni</i>		72			
	<i>Halosauropsis macrochir</i>	21	Perciformes (Zoarcidae)		<i>Lycenchelys alba</i>	73		
	<i>Halosaurus johnsonianus</i>	22			<i>Lycenchelys paxilla</i>	74		
	<i>Halosaurus ovenii</i>	23			<i>Lycodes atlanticus</i>	75		
	<i>Notacanthus bonapartei</i>	24			<i>Lycodes esmarkii</i>	76		
	<i>Notacanthus chemnitzii</i>	25			<i>Lycodes pallidus</i>	77		
	<i>Polyacanthonotus challengerii</i>	26			<i>Lycodes vahlii</i>	78		
	<i>Polyacanthonotus merretti</i>	27			<i>Lycodonus mirabilis</i>	79		
	<i>Polyacanthonotus rissoanus</i>	28			<i>Melanostigma atlanticum</i>	80		
Figure 9								
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	<i>Alepocephalus bairdi</i>	30	Beryciformes	<i>Lophius piscatorius</i>		82		
	<i>Alepocephalus productus</i>	31		<i>Hoplostethus mediterraneus</i>		83		
	<i>Alepocephalus rostratus</i>	32		<i>Acanthochaenus luetkeni</i>		84		
	<i>Bathytroctes microlepis</i>	33		Syngnathiformes		<i>Macrorhamphosus scolopax</i>	85	
	<i>Conocara macroptera</i>	34				Scorpaeniformes	<i>Sebastes norvegicus</i>	86
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	<i>Leptoderma macrops</i>	37					<i>Cottunculus thompsoni</i>	89
	<i>Narctes stomias</i>	38					<i>Leptagonus decagonus</i>	90
	<i>Rinoctes nasutus</i>	39					<i>Paraliparis hystrix</i>	91
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	<i>Xenodermichthys copei</i>	42				<i>Hippoglossus hippoglossus</i>	94	
Aulopiformes	<i>Bathymicrops regis</i>	43	<i>Reinhardtius hippoglossoides</i>		95			
	<i>Bathypterois longipes</i>	44						
	<i>Bathypterois quadrifilis</i>	45						
	<i>Bathytyphlops sewelli</i>	46						
	<i>Ipnops agassizii</i>	47						
	<i>Ipnops murrayi</i>	48						
<i>Bathsaurus ferox</i>	49							