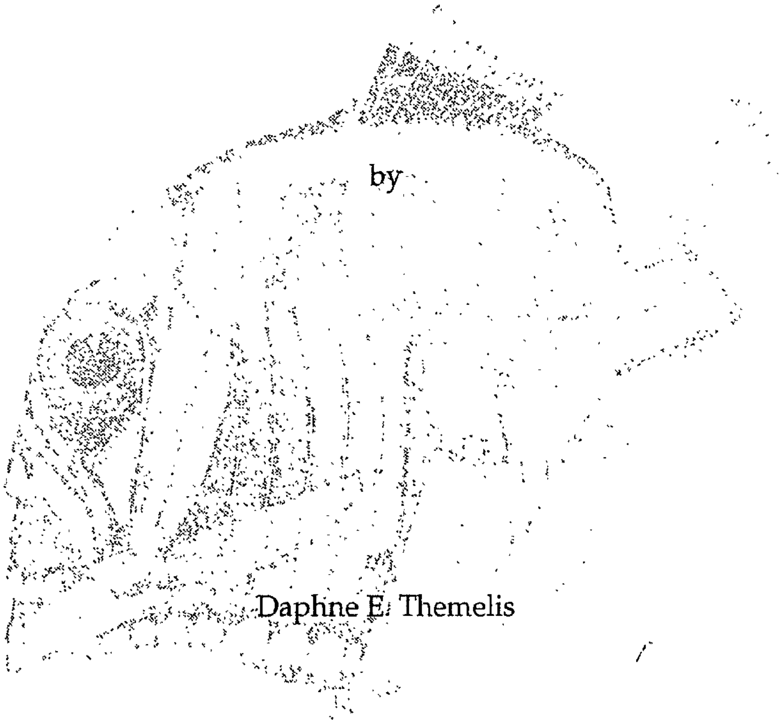
Variations in the abundance and distribution of mesopelagic fishes in the Slope Sea off Atlantic Canada



by

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Abstract

Seasonal variations in the composition, structure, and spatial and vertical distribution patterns of the mesopelagic fish fauna in the Slope Sea off Atlantic Canada were studied from data obtained during ten midwater trawl surveys sampling at depths 0-1000 m between October 1984 and August 1989 to determine if a distinct and persistent fauna was present. In total, 227 species in 40 families were captured. Few species were very abundant or occurred frequently; 143 were rare (< 16 specimens), only seven species occurred in more than 75% of the 302 tows and three myctophid species, *Ceratoscopelus maderensis*, *Benthosema glaciale*, and *Lobianchia dofleini* comprised 70% of 239,412 fish caught. Faunal structure varied seasonally as species richness and evenness was lower in winter-spring surveys when *B. glaciale* or *C. maderensis* predominated, than in the summer-fall surveys when *L. dofleini* or *Hygophum hygomii* was most abundant. Diel vertical profiles (0-600 m) in April showed the fauna migrated from depths > 300 m in the day to < 200 m at night, except *Cyclothone* which remained at depths > 300 m. Ordination of species data from six seasonal surveys indicated a faunal gradient of decreasing species richness and evenness which was significantly correlated with decreasing temperature and salinity in the upper 200 m. Classification analysis resulted in two or three station groups corresponding to three water masses: Warm Core Rings (Gulf Stream), Warm Slope Water (WSW) and Labrador Slope Water. Faunal differences were due to changes in abundance across the water mass boundaries rather than disjunct distributions. Three interacting mechanisms are proposed to explain the seasonal variation in faunal structure: 1. continuous advection of water and fauna by the Labrador Current and Gulf Stream into the Slope Sea; 2. seasonal abundance cycles of subtropical species with one year lifespans; 3. seasonal cooling of the WSW which decreases the reproductive success of invading subtropical species, thus requiring them to recolonize the WSW most years. The WSW fauna is persistent and distinct in structure from those of the adjacent water masses.

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Two friends, Rod Bradford and and Mark Showell, gave me special support and encouragement. Finally, I am grateful to my parents Nickolas Themelis and the late Doris Irwin, and most of all, to my husband Peter Hurley for encouraging me to finish this, and for keeping me together.

Chapter 1: General Introduction

Mesopelagic fish species live at depths between about 150 and 1000 m (Marshall 1971). Most are small relative to coastal species, reaching maximum sizes between 1.5 and 20 cm. Many species have morphological features not seen in coastal species, such as photophores and/or phosphorescent tissue, complex barbels and fanged teeth. Their ability to actively counter the effects of oceanic currents on their horizontal distributions is uncertain so they are usually referred to as micronekton. The major families are the Myctophidae (lanternfishes) and Gonostomatidae. Other important families are the Sternoptychidae, Photychthyidae, Chauliodontidae and Stomiidae.

A major portion of the fish biomass in oceanic areas is composed of mesopelagic species (Clarke 1973; Mann 1984). Density is generally low, for example, biomass in the Northwest Atlantic is 0.05-0.2 g/m^2, as estimated from small trawls sampling from surface to 200 m depths (Gjosaeter and Kawaguchi 1980). These species may be important in the vertical transfer of energy since many species migrate diurnally to feed in the more productive epipelagic zone (Merrett and Roe 1974; Hopkins and Baird 1977; Vinogradov and Tseitlin 1983). Mesopelagic fish are consumed by a variety of predators, including birds, fish and cetaceans (e.g. Gjosaeter and Kawaguchi 1980; Robison and Craddock 1983; Ainley et al. 1986; Walker and Nichols 1993) and also contribute organically rich faecal material to bathypelagic and benthic habitats (Robison and Bailey 1981). Due to their small size, low density and difficulty in capture, mesopelagic fishes have only recently become commercially interesting. Lanternfish densities are high enough to support commercial fisheries at a few locations off South Africa, and in the Indian and Southern Oceans (FAO Yearbook 1994). Generally, fish meal, oil and fish silage are produced, although some fish have been taken for human consumption (Gjosaeter and Kawaguchi 1980).

1.1 Review of mesopelagic fish surveys

Early surveys were limited to information on the taxonomy and distribution of individual species (e.g. Morrow 1964; Backus et al. 1965, 1969, 1970; Nafpaktitis 1968, 1973; Krefft 1974; Hulley 1981; Nafpaktitis et al. 1977). Comparisons of the distribution patterns of individual species from these large-scale surveys indicated conformity between broad zoogeographic patterns and major oceanographic features. Faunal discontinuities were often associated with the areas of rapid hydrographic changes occurring between water masses. These observations led to the application of a hypothesis already developed from observations on other taxonomic groups: that pelagic species distributions conformed to the boundaries of the water masses as defined by their temperature-salinity characteristics. Studies on several taxonomic groups in the Pacific have indicated a degree of conformity by species assemblages to the large central gyres (McGowan 1974, 1977; Barnett 1983, 1984). However, species distributions in the Atlantic are more complex.

Distribution patterns differed among species and families as some species were restricted to a portion of a water mass while others ranged over more than one water mass (Backus et al. 1969; Backus 1986). Haedrich and Judkins (1979) summarise the early evidence in support of the theory, indicating that it was insufficient to explain many zoogeographic patterns.

The water mass hypothesis may fail to provide an adequate description of midwater fish distributions because water masses are described by subsurface hydrographic properties. Mesopelagic species must be influenced by the localised or large-scale events occurring at the surface since many of their activities such as feeding (Hopkins and Baird 1977), reproduction (Gjosaeter and Tilseth 1988; Robertson 1977; Gartner 1993) and larval development (Loeb 1979; Sabates 1991) occur within the upper 100 metres. A number of physical, chemical and biological characteristics associated with the water column have been used to explain the distributions of mesopelagic species. These include oxygen content, upwelling and primary production, thermal fronts and currents, light regimes, and temperature or salinity structure (Haffner 1952; Ebeling 1962; Paxton 1967; Robison 1972; Dalpadado and Gjosaeter 1987; Backus et al. 1965, 1969, 1970, 1977, Haedrich 1972; Hartman and Clarke 1974; Jahn 1976; Jahn and Backus 1976; Badcock and Merrett 1977; Badcock 1981; Brandt 1981, 1983, Hulley 1981; Barnett 1983, 1984; Willis 1984; Griffiths and Wadley 1986; Clarke 1987; Zelck and Klein 1995). Species distributions on the continental slopes may also be affected by bottom depth and associated water currents, primary production, thermal structure and light regimes (e.g., Musick 1973; Badcock 1981; May and Blaber 1989; Reid et al. 1991; Hulley 1992).

Recent distribution studies used multivariate techniques to define faunal assemblages and determine the extent to which oceanic fronts act as faunal boundaries (e.g. Hartman and Clarke 1975; Robertson et al. 1978; Jahn and Backus 1976; Brandt 1983; Barnett 1983, 1984; Willis 1984; Sabates 1990). Samples clustered into a few groups containing distinctive faunas. Classifying species usually results in many groups which each contain only a few species (Haedrich and Judkins 1979; Karnella 1987), meaning that the distribution ranges of several species overlap, but few are congruent. McKelvie (1985a) argued that discrete faunal groups may be an artifact of analytical methods such as classification and recurrent group analysis. He used ordination to demonstrate that faunal change in the Northwest Atlantic was graded, and speculated that the phenomenon was due to individual species responses to physical gradients. Zonation of mesopelagic and benthopelagic species over slopes have been observed (Badcock 1981; Merrett 1986; Reid et al. 1991), although Hulley (1992) suggests that these may be localized artifacts created by interaction between depth and temperature structure of the water column.

The occurrence of structured demersal fish communities in the deep-sea has been questioned by Haedrich and Merrett (1990, although this has been challenged recently by Koslow 1993; Koslow et al. 1994). These authors argued that zonation with depth was only evident at a local scale. Perception of deep-sea community structure has shifted from viewing them as areas of slow faunal change bordered by regions of rapid faunal change (Haedrich et al. 1980) to groups of species displaying regular and continuous turnover along gradients (e.g. Sulak 1982; Stefanescu et al. 1991). Faunal discontinuities may be mainly artifacts of sampling, analytical methods, or may relate to local phenomena caused by abrupt physical variability in the environment.

Most mesopelagic distribution studies have been based upon geographically extensive surveys sampling at widely spaced sites without repetition. Few provide a comprehensive view of the faunal composition or patterns within a region. Spatially and temporally frequent sampling is needed to measure variability in species composition and relative abundance, and determine whether faunal structure is temporally consistent. The effects of hydrographic fronts on species distributions can only be considered from closely spaced samples across the fronts. Intensive sampling programs can secondarily provide valuable information on life histories and ecology (e.g. Goodyear et al. 1971; Gibbs et al. 1972; Howell and Krueger 1987; Karnella 1987; Gartner 1993; Hopkins and Gartner 1992).

1.2 Previous descriptions of the mesopelagic fish fauna of the Slope Sea

The Slope Sea is the narrow band of ocean lying between the continental shelf and the Gulf Stream extending from Cape Hatteras to the

Grand Banks (Fig. 1.1; Csanady and Hamilton 1988). The Slope Sea has been referred to as Slope Water in earlier mesopelagic studies of this region. The taxonomic composition and relative abundance of the mesopelagic fish fauna in the Slope Sea adjacent to the continental shelf of Nova Scotia is poorly described. Only a few studies have sampled beyond the 1000 m contour of the continental slope or focused on mesopelagic species. Most records are the ancillary results of research directed at commercial fish and squid species, such as feeding studies, larval distribution surveys and trawling surveys, or are specimens taken as bycatch in commercial fisheries. Surveys directly sampling for mesopelagic species in the Slope Sea were primarily interested in species distributions and their physical correlates (Backus et al. 1970, 1977; Jahn 1976; Jahn and Backus 1976; Backus and Craddock 1982; Evseenko 1982; Wroblewski and Cheney 1984; McKelvie 1985a).

These records (most recently summarised in Scott and Scott 1988) indicate a rich fauna of species with subarctic through tropical Atlantic origins, but estimates of the relative abundance of species are unreliable. Backus and co-workers examined aspects of the faunal structure (species richness, diversity indices and dominant species), but their surveys were largely restricted to the western end of the Slope Sea. Only McKelvie (1985a) examined more than a few samples from the region adjacent to the Scotian Shelf. No seasonal comparisons of the faunal structure have been made, nor have the directed surveys resulted in a comprehensive mesopelagic fish species list for the Slope

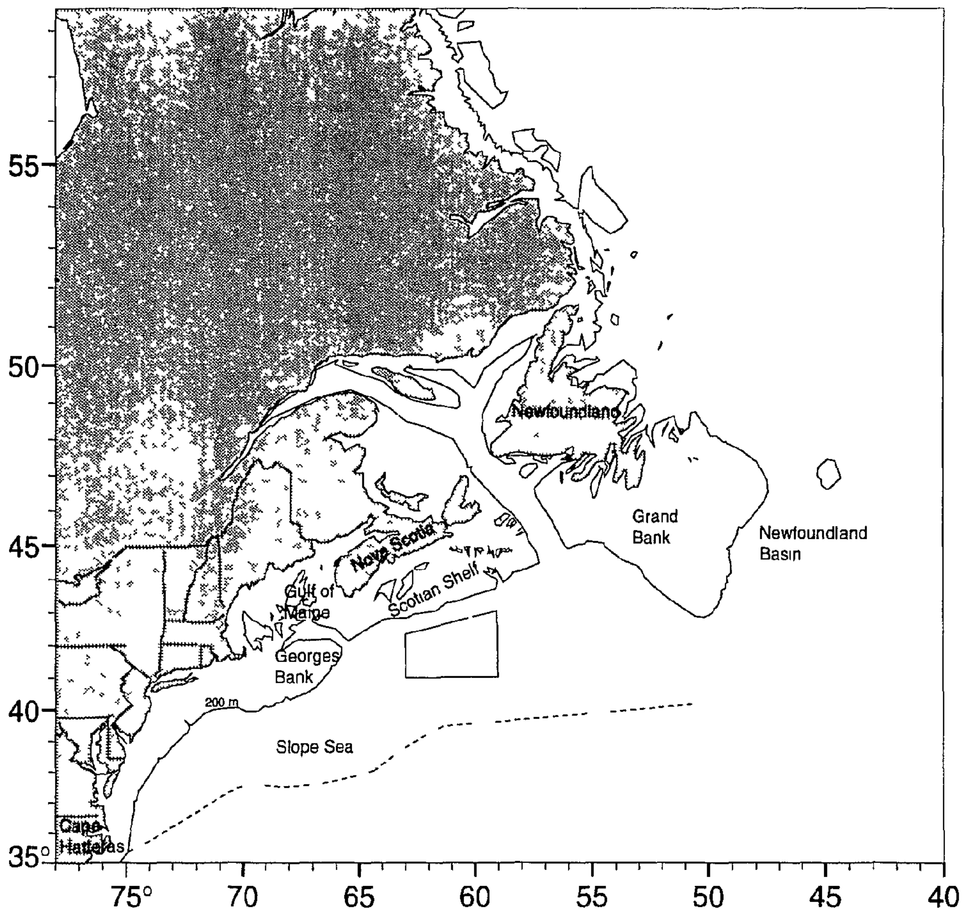


Figure 1.1. Geography of the eastern coast of North America and the relative position of the Slope Sea and study area. The box indicates the area sampled by the six standard cruises.

Sea. Backus et al. (1977) included Slope Sea samples in their summary of the myctophid component of the fauna of the North Atlantic Temperate Region. McKelvie (1985b) described the fauna of the Newfoundland Basin (Fig. 1.1), a more northerly region which may inject species into the Slope Sea through the Labrador Current (McKelvie 1985a).

1.3 The present study

This thesis addresses two competing hypotheses on the nature of the mesopelagic fish fauna associated with the Slope Sea. These are: 1) that this region supports a characteristic and persistent mesopelagic fish fauna, or 2) this region is simply a transition area between adjacent faunal zones. Addressing these alternative hypotheses required describing the species composition of the fauna, examining spatial and temporal variations in distribution patterns and abundances of the more abundant species, and evaluating the importance of physical factors as potential determinants of these species attributes. An intensive sampling program was necessary to achieve these secondary objectives, requiring several design decisions with regards to the choice of sampling method (gear, towing depth and diurnal period), frequency (number of repeated tows, number of surveys) and location (whether to sample well within the water masses or at the fronts). The rationale behind these decisions is discussed below.

1.3.1 Sampling gear

The two trawls chosen for this study were a relatively large IYGPT (International Young Gadoid Pelagic Trawl) and a small Tucker trawl. Most samples were taken with the IYGPT (approximate mouth area of 100 m^2). Since the IYGPT is inefficient at capturing organisms <25 mm length (Potter et al. 1990), some locations were also sampled with the Tucker trawl (mouth area 2.5 m^2) equipped with an opening-closing device. Catches from this trawl were used to make inferences about the gear deployment strategy and sampling characteristics of the more frequently used IYGPT.

Differences in size of the trawls were intended to alleviate the effects of avoidance and escapement on the efficiency of a towed net. Larger members of a given species may be better able to avoid small nets. Small individuals are more likely to escape through the wide meshes surrounding the mouths of large trawls, and diminutive species may not be represented in catches as a result. Reviews of sampling gear for micronekton warn that a variety of nets is preferable because no net can accurately sample all species in all size ranges (Harrisson 1967; Angel 1977; Kashkin and Parin 1983; Pearcy 1983). The most frequently used nets have mouth openings of 1-10 m^2; examples of these and the studies employing them are the Isaac-Kidd Midwater Trawl (IKMT, Badcock 1970; Gibbs et al. 1971; Clarke 1973; Jahn and Backus 1976; Barnett 1983, 1984; Gartner et al. 1989), Tucker Trawl (Davies and Barham 1969; ; Gartner et al. 1987, 1988), Rectangular Midwater Trawl (RMT, Clarke 1969;

1983, 1984; Gartner et al. 1989), Tucker Trawl (Davies and Barham 1969; ; Gartner et al. 1987, 1988), Rectangular Midwater Trawl (RMT, Clarke 1969; Badcock and Merrett 1976; Kawaguchi and Mauchline 1982; Brandt 1981, 1983), MOCNESS (Craddock et al. 1992) and BIONESS (Sameoto 1988). Most of these can be equipped with combinations of opening-closing devices on the mouth or codend, multiple nets, and equipment to monitor net behaviour during towing and the amount of water filtered. Few studies use commercial sized trawls (mouth openings of 50-700 m^2) because they require vessels with stern ramps and specialized winches (Pearcy 1983). Large trawls are reported to capture larger individuals and more species than small trawls (Pearcy 1980; Kashkin and Parin 1983). They also filter more water per tow which is advantageous in the sparsely and patchily populated environment of the mesopelagic zone (Backus et al. 1968; Wiebe 1971; Pearcy 1983). However, small trawls catch greater numbers of fish per unit time and are often more appropriate for life history studies because they capture smaller and earlier life stages (Clarke 1973; Gartner et al. 1988).

1.3.2 Sampling depth

Choice of an appropriate towing depth must consider the vertical mobility of the mesopelagic fauna. During the day, most mesopelagic species occur below depths of 200 m (Pearcy and Laurs 1966; Pearcy et al. 1977). At night, individual species may vertically migrate to the surface, intermediate depths, or not migrate at all (Badcock 1970; Badcock and Merrett 1976).

Daytime and nighttime depths of maximum abundance are species specific and only a portion of the population may migrate on a given night (Paxton 1967; Pearcy et al. 1977). Many species also undergo an ontogenetic migration (Gibbs et al. 1971; Clarke 1973; Badcock and Merrett 1976; Loeb 1979; Willis and Pearcy 1980; Ropke 1993): the larvae hatch near the surface and descend as they develop, newly metamorphosed juveniles may occur deeper than the daytime depth of adults, and adults may occupy deeper night and day depths as they grow larger. Several studies have noted latitudinal variations in species-specific vertical ranges and related them to preferences in temperature (Jahn 1976; Badcock and Merrett 1977; Albikovskaya 1988) and light levels (Marshall 1971; Roe 1974) or interactions between these variables (Paxton 1967), primary productivity (Kinzer 1977; Sameoto 1988) and interspecific relations (Miya and Nemoto 1986). The rationale behind towing depths is unclear in some studies and explicit in others. For example, Backus et al. (1965, 1966, 1969, 1970) maximized the catch at each site by sampling where midwater fish were concentrated: at positions of sound-scattering maxima, temperature inversions and bottoms of thermoclines. They point out that pressure is the only physical factor standardized by sampling at a fixed depth over a wide geographic area (Backus et al. 1965). Kashkin and Parin (1983) recommend oblique tows as a sampling method which integrates catches over a wide vertical range while minimizing effort.

In this study, a standard tow with the IYGPT was defined as a three ten minutes at each step, during hours of darkness only when most of the more abundant mesopelagic species were expected to occur in this zone (Backus et al. 1970). These tows provided the primary data for analysis of geographic and temporal distributions. The tows could be executed quite efficiently, maximizing the number of tows which could be conducted each night. However, they provided no information on vertical distributions, and resulted in a biased view of species composition because of the characteristics of the trawl and towing strategy. Thus, two additional sampling strategies were used to ensure that species not available to night stepped oblique tows were also sampled. The IYGPT was towed at discrete depths > 300 m during the day to capture non-migratory or partially migrating species and individuals. Also, variations in the vertical distribution of the fauna were investigated by deploying the Tucker Trawl at discrete depths between 50 and 600 m.

1.3.3 Sampling location and survey frequency

Previous studies of the horizontal distributions of the mesopelagic species in the Slope Sea indicated the presence of discrete faunal groups, the positions of which were correlated with the water masses (described in the following section) occurring over the continental slope (Jahn and Backus 1976; Jahn 1976; Backus and Craddock 1982). ploratory surveys over the continental slope off Nova Scotia in 1984 and 1986 by the Department of

Fisheries and Oceans also indicated clear faunal transitions (i.e. changes in dominant species, relative abundance) across the front between the cold, low salinity water which occupies the northeastern part of the Slope Sea and the warm, high salinity water in the south and west. Shortly after the surveys comprising this research were begun, a study by McKelvie (1985a) questioned the presence of discrete mesopelagic faunal groups off the Scotian Shelf. He argued that his analysis of samples from the Slope Sea off Nova Scotia and more northerly areas showed a gradation between the faunas of the Gulf Stream and Newfoundland Basin (Labrador Current), and that the Slope Water was an ecotone or transition zone with no characteristic fauna of its own.

Two types of surveys were used to sample the mesopelagic fauna during the present study. The first four surveys were exploratory: their primary objective was to qualitatively characterise the fauna by sampling at variable geographic locations, depths and water types in the central and eastern part of the Slope Sea which lies between the western edge of the Scotian Shelf and the western edge of the Grand Banks. The subsequent six surveys sampled along fixed transects running seaward from the edge of the central part of the Scotian Shelf. Collectively, these latter surveys provided a view of the mesopelagic fauna of the central Slope Sea in every second month of the year. Most samples were regularly spaced to document any changes in species composition or relative abundance occurring across the hydrographic fronts.

1.4 Oceanography of the Slope Sea

Slope Water, the major water mass occupying the Slope Sea, has two components: Warm Slope Water (WSW) which occupies the southwestern portion of the Slope Sea, and Labrador Slope Water (LSW) which occupies the northeastern portion and rarely extends to south of Georges Bank (Fig 1.2). Slope Water is bounded on the north and west by Shelf Water (SHW), and to the northeast by the Labrador Current which flows into the Slope Sea over and around the Grand Bank (Fig 1.2). To the south is the Gulf Stream (GS) which forms the western edge of a large subtropical gyre enclosing the Sargasso Sea (Fig 1.2). Water flowing westward through the Caribbean Sea passes through the Florida Straits and, joined by the Antilles Current, flows northward along the continental slope. At Cape Hatteras, it is diverted away from the slope and moves in a generally northeast direction over oceanic depths. The GS branches northeast of Newfoundland, where part of it mixes with Slope Water and flows north as the North Atlantic Current (Mann 1967), while the rest turns south to complete the gyre. Large meanders pinching off north (south) of the GS form warm (cold) core rings. Warm core rings (WCR) consist of a band of Gulf Stream Water flowing clockwise around a centre of Sargasso Sea Water. They are 100-200 km wide, and as deep as 1500 m. Rings are variable in their location, lifespan and direction of movement. Trites and Drinkwater (1990) and Drinkwater and Trites (1991) report 28 and 32 warm core rings between 75 °W and 45 °W during 1988 and 1989, respectively, with lifespans

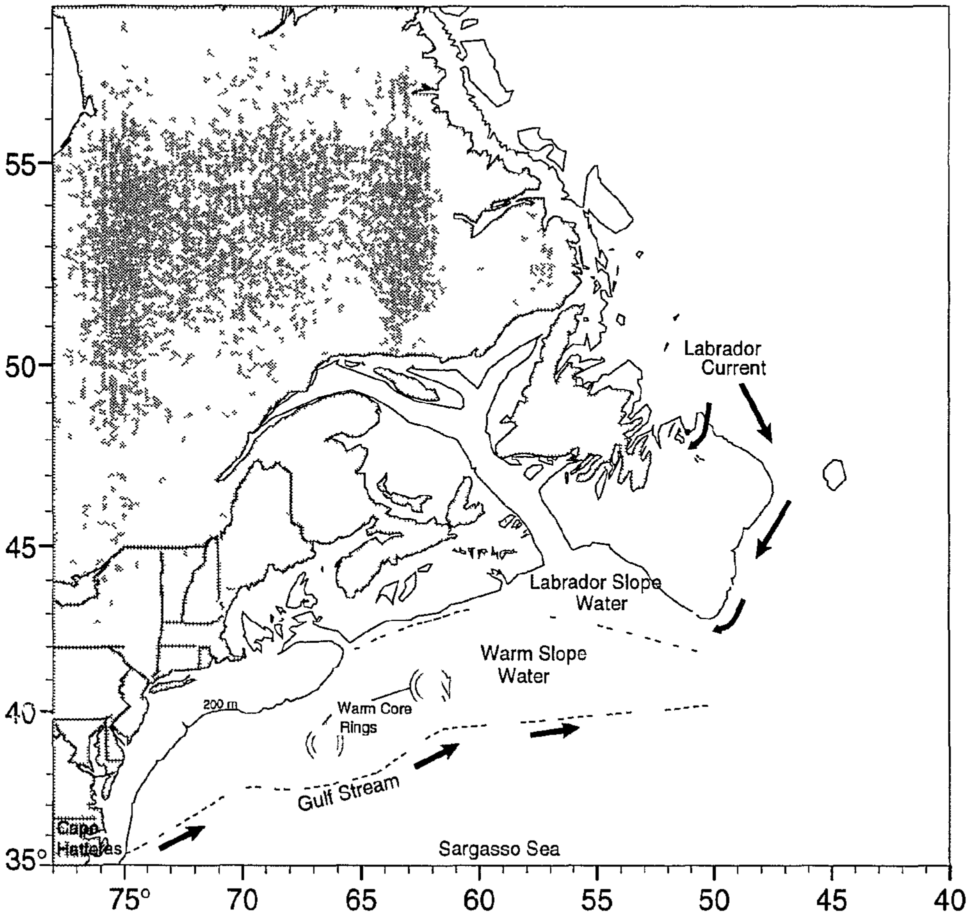


Figure 1. 2 Major oceanographic features within and adjacent to the Slope Sea (after Csanady and Hamilton 1988)

ranging from two weeks to more than a year and an average of 3 months for both years.

Each water mass is discernible by its temperature and salinity characteristics, although these may be seasonally and spatially variable SHW is a surface water mass of about 50-100 m depth, with a salinity < 33 5, which extends out from the continental shelf over the LSW and part of the WSW (labelled Coastal Water in Fig. 1 3) In the winter, the boundary (or front) between SHW and WSW is apparent as a rapid change in temperature by several degrees over a few kilometres In summer, surface temperatures of WSW and SHW are similar and salinity becomes a better indicator of the SHW/WSW front. The LSW is discernible as subsurface water adjacent to the shelf edge < 10 °C and fresher than 35 (Fig 1 3) WSW is a 300-400 m deep water mass lying over North Atlantic Central Water (NACW, Gatien 1976, Fig 1.3). Temperature of the upper 200 m vary seasonally, ranging from 4-12 °C in February to 11-25 °C in August during the present study. Salinity also varied from 34.0 to 35.9 in the upper 200 m during this study Below 200 m, a permanent thermocline extends from 200-500 m within which temperatures decline from 10-14 °C to 5 °C. The GS is warmer and more saline than WSW and the front is indicated by a steep downward trend in isotherms as, for example, the 15 °C isotherm descends from near the surface to greater than 200 m depths, while salinity is > 36 A newly formed WCR is detectable by surface salinities > 36, rapidly descending isotherms, and temperatures > 15 °C

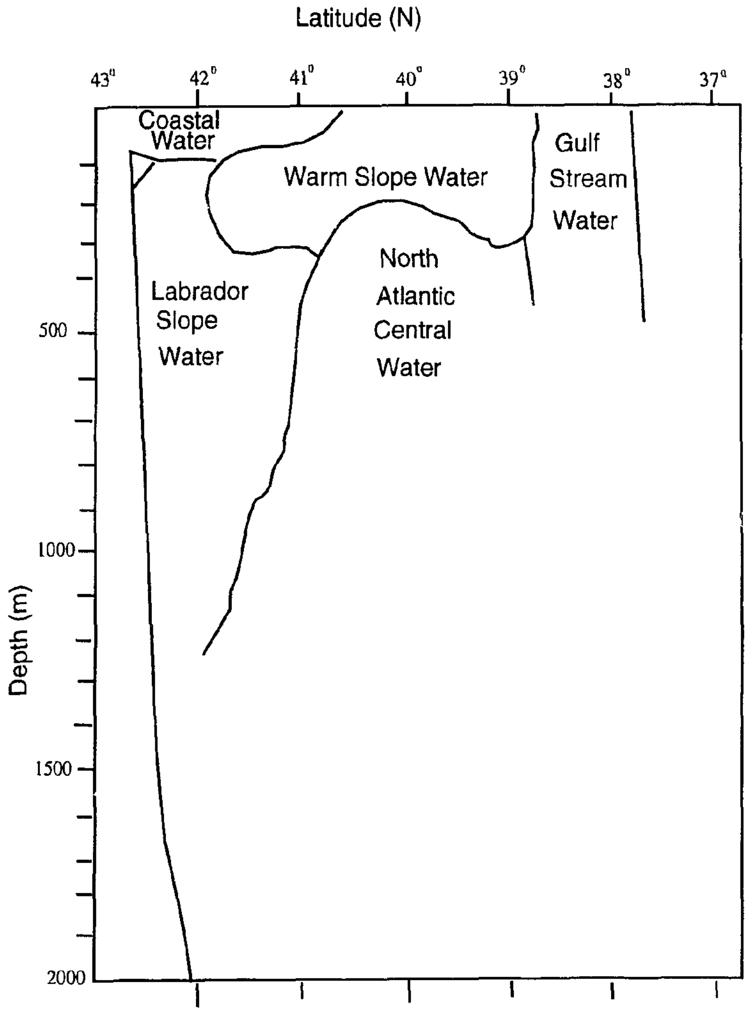


Figure 1.3. Approximate positions and vertical extent of the water masses along 64 30 ' W during the Gulf Stream '60 survey (from Gatien 1976).

at 200 m, but its characteristics reflect those of the surrounding WSW as it ages (Joyce and Wiebe 1983).

Boundaries between the SHW, LSW, WSW and GS are horizontally convoluted and variable in position. The monthly mean position of the SHW/WSW boundary in the study area ranges 80 km interannually, and 40 km seasonally, occurring closest to the shelf edge in August through October and furthest offshore in the winter, based upon twenty years of observations (Drinkwater et al. 1994). Seaward displacement of the SHW/WSW front occurs frequently along the Scotian Shelf and Georges Bank and is usually associated with WCRs (Halliwell and Mooers 1979). The monthly mean position of the WSW/GS boundary ranges about 20 km seasonally, with a maximum onshore position in October-November, but the range in displacement interannually is about 80 km (Auer 1987; Drinkwater et al. 1994). Analysis of oceanographic data collected during this study, and comparisons with temperature measurements from concurrent satellite images, indicated that all fronts moved substantially over a period of a few days.

The LSW, WSW and SHW are formed from different proportions of the same source waters. Shelf Water is composed of water from the Labrador Current as well as runoff from the continental shelf. The LSW is an incompletely mixed combination of Labrador Current and NACW, which becomes warmer and more saline (more like WSW) as it moves westward (Gatien 1976). Deep WSW (> 200 m) is formed from a 4:1 ratio of Labrador

Current and NACW (McLellan 1957). The fronts between the LSW/WSW and SHW/WSW are regions of intense interleaving (Horne 1978). The surface layer of the WSW has as its sources SHW and GS water. Meanders of the GS draw SHW into the Slope Water as filaments or parcels (Schmitz et al. 1987) and result in the discharge of GS water into the Slope Water (Churchill et al. 1993). The extent of interaction between WCR and the SHW or WSW can be substantial. As a ring approaches the shelf edge, it disrupts the SHW/WSW front by entraining SHW around its northeastern side (Halliwell and Mooers 1979). Most rings are destroyed by contact with another ring or resorbed by the Gulf Stream, but a substantial proportion of long lived rings may become mixed into the WSW (Craddock et al. 1992).

This study followed the conventions set in previous studies on midwater fish distributions in the Northwest Atlantic by defining the water masses by the temperature at 200 m: LSW < 9 °C; 9 °C ≤ WSW < 15 °C; GS ≥ 15 °C (Jahn and Backus 1976). In the present study, Shelf Water had salinity < 34.5, and the SHW/WSW front was the zone in which surface temperature (at least in winter and spring) and salinity changed rapidly. WCRs were distinguished from GS by reference to National Oceanic and Atmospheric Agency oceanographic analyses of satellite images and sea surface temperature observations coincident with a given mesopelagic survey cruise. Sargasso Sea Water was distinguished within a WCR in a June survey (N122) as water of > 18 °C at 200 m.

1.5 Organization of the thesis

Chapter 2 presents an examination of the composition and relative abundance of the mesopelagic fauna of the Slope Sea adjacent to Nova Scotia, based solely upon IYGPT tows at depths between 50 and 1000 m. In Chapter 3, the vertical distribution of the fauna captured by the Tucker Trawl samples at three time intervals is described and contrasted to tows in the same location by the IYGPT. Chapter 4 compares distribution patterns of the fauna in six bimonthly surveys of the Slope Sea and relates these to observed physical features of the water masses. Conclusions based upon earlier surveys are re-examined through use of multivariate techniques, to determine if changes in the composition of the mesopelagic fauna are gradual and continuous with increasing distance seaward, or if the fauna partitioned into discrete zones, and whether any observed zones are correlated with the positions of the water masses. Chapter 5 summarises the results of the study with reference to the original, general objectives stated on page 8.

Chapter 2: Species composition and relative abundance of the mesopelagic fish fauna in the Slope Sea off Atlantic Canada

2.1 Introduction

The composition and structure of the mesopelagic fauna off the Scotian Shelf is poorly described because few surveys have been designed specifically to sample that fauna. Species composition has been documented mainly through incidental catches of midwater species on the Scotian Shelf and shelf break by diverse sampling gears such as stomach contents, longlines, midwater and bottom trawls (Leim and Scott 1966; Halliday and Scott 1969; McKelvie and Haedrich 1985), neuston and bongo nets (Markle et al. 1980). A few ichthyoplankton surveys have sampled seaward of the 1000 m depth contour (Evseenko 1982; Wroblewski and Cheney 1984). These records, most recently summarized in Scott and Scott (1988), indicate a diverse fauna composed of species with subarctic through tropical origins.

Few research programmes have examined the structure of this regional fauna. Backus et al. (1970) estimated the abundance, biomass and diversity of midwater fishes in the Slope water based upon five tows with a small midwater trawl. Jahn and Backus (1976) compared the relative abundances of midwater species between the Slope Water, Gulf Stream and northern Sargasso Sea. The mesopelagic fish fauna in the Slope Water and Gulf Stream adjacent to the Scotian Shelf, and in the Newfoundland Basin was described and compared by McKelvie (1985a, 1985b). A general description of fauna diversity cannot be obtained by combining the observations of Backus and colleagues with those of McKelvie because of differences in fishing gear, sampling depths, time of year and presentation of their results. These studies were primarily interested in faunal zonation so they catalogue differences in relative abundances of dominant species between water masses (described in Chapter 1) collected within a short time period (McKelvie 1985a), or after combining samples taken over several months (Jahn and Backus 1976).

This chapter describes the mesopelagic fish fauna in the Slope Sea off the Scotian Shelf and its seasonal and spatial variation. The present study is the first to systematically survey the area in this fashion. Areas sampled overlap those sampled by Jahn and Backus (1976) and McKelvie (1985a).

2.2 Methods

Ten cruises were conducted by the Department of Fisheries and Oceans in the slope region off Nova Scotia between October 1984 and August 1989 using the MV Lady Hammond (H) and the MV Alfred Needler (N)(Table 2.1). The first four cruises were designed to be exploratory and were therefore geographically extensive. Six subsequent 'standard' cruises examined spatial and seasonal variability in fish distributions using a standard protocol and sampling regularly along fixed transects. Total area sampled extended to the western edge of the Grand Bank (cruise N089), into the Gulf Stream (N057),

Table 2.1. Cruise by designation and date; showing the numbers of samples in each cruise, the numbers of shallow (< 299 m tow depth) night and other tows, and maximum depth of other tows (H - MV *Lady Hammond*, N - MV *Alfred Needler*).

Cruise	Designation	Date	No. Shallow Tows	No. Other Tows	Max Tow Depth
H127	Exploratory	Oct 24-Nov 5/84	11	2	900
N057	Exploratory	Feb 10-Feb 19/86	18	1	1000
N067	Exploratory	Aug 25-Sept 5/86	38	0	290
N089	Exploratory	Sept 23-Sept 30/87	28	4	1000
N096	Standard	Feb 17-Feb 25/88	26	10	1000
N110	Standard	Oct 18-Oct 26/88	34	10	1000
N112	Standard	Nov 30-Dec 8/88	35	16	1001
N119	Standard	Apr 12-Apr 20/89	15	7	627
N122	Standard	June 6-June 15/89	18	8	950
N126	Standard	Aug 10-Aug 18/89	21	0	298

and adjacent to the eastern and western portions of the Scotian Shelf (N067 and H127, respectively, Fig 2.1). The numbers of samples differed among cruises (Table 2.1) due to variability in day length, position of the oceanographic fronts, gear breakdown and storms. Collectively, the standard cruises provide a view of the midwater fauna at two month intervals.

2.2.1 Sampling Protocol

Sampling protocol differed between diurnal (from one hour after sunrise to one hour before sunset) and nocturnal (one hour after sunset to one hour before sunrise) periods. At night, sites were sampled systematically by tows along transects at 10-15 mile intervals with the sampling frequency dependent on the number of hours available. Tows were irregular during day periods. A few tows were made during sunrise and sunset by accident of mistiming but the intention was to avoid sampling during these periods.

Stations were sampled with an International Young Gadoid Pelagic Trawl (IYGPT: Hislop 1970; Koeller and Carrothers 1981), a midwater trawl equipped with 48 deep-sea floats of 20 cm diameter rated to 1400 m depth. The codend was knotless nylon with a stretched mesh size of 1.25 cm. The mouth opening averaged 8.5 m high and 11.5 m wide while towed, as indicated by electronic telemetering units (SCANMAR) placed on the headrope and wings.

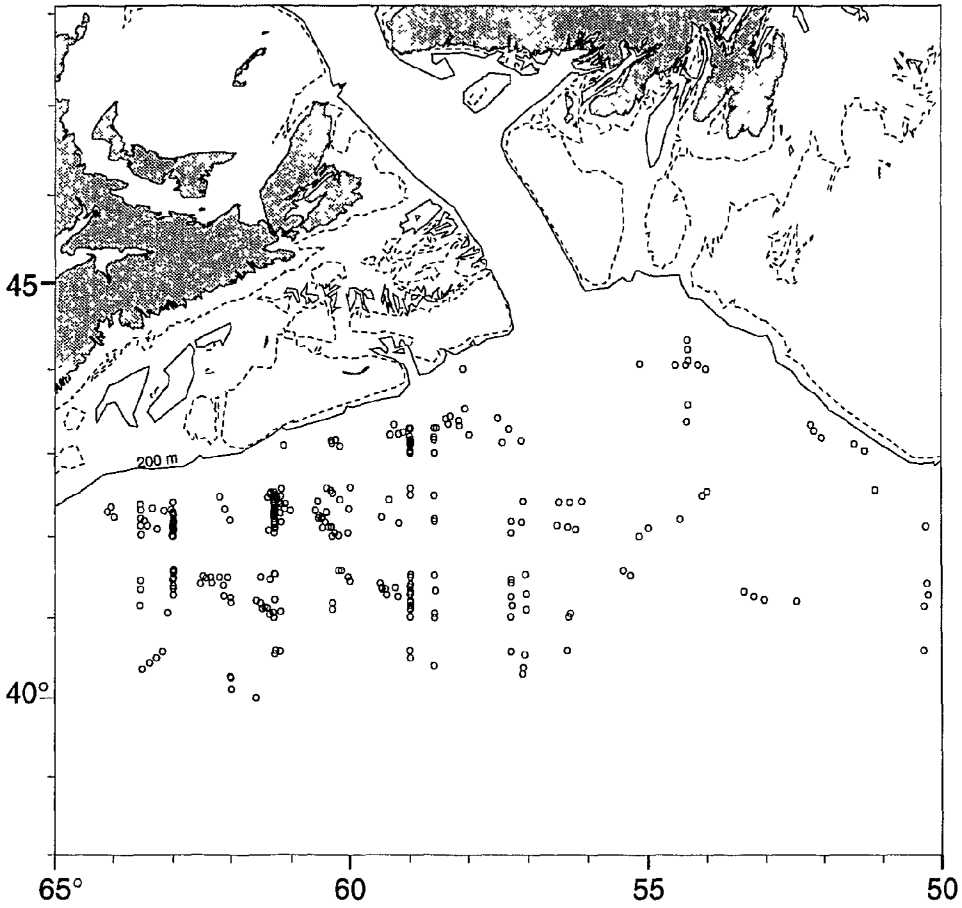


Figure 2.1. Location of mesopelagic sampling during ten surveys of the Slope Sea between 1984 and 1989.

The IYGPT was set by releasing the required warp and then increasing ship speed to position the net at the desired depth. SCANMAR units on the trawl indicated that the net opened soon after ship's speed increased, and remained open through both the horizontal tow and retrieval of the warp to within at least 20 m from the surface. Timing of the tow began when the net was about 20 m shallower than the desired depth. Ship's speed was maintained at 2.5 knots as determined by Loran C. Tows at less than 600 m depth were monitored by a midwater trawl headline transducer on the first six cruises, and SCANMAR on the following four. A Time-Depth Recorder (TDR; maximum depth reading of 1000 m) provided depth information on deeper tows and when the other systems failed. Tow depths were maintained through adjustment to ship's speed and were generally within 10% of the desired depth.

Day tows were horizontal tows of 30 minutes duration at depths usually greater than 300 m. Most night tows were stepped oblique, but a horizontal 30 minute 300 m tow was conducted following the stepped oblique tow at the boundary between Labrador Slope Water (LSW) and Warm Slope Water (WSW) on a few occasions. Also, 30 minute horizontal tows at 50, 100 and 200 m depths were made at night on three occasions for comparison with stepped oblique tows and a small Tucker trawl. On night stepped oblique tows, the net was towed sequentially at two or more depths, for a total (horizontal) set time of 30 minutes. Stepped oblique tows on exploratory cruises N067 and

N089 were three steps at 190-228 m, 110-155 m and 45-60 m. Cruises H127 and N057 used a similar strategy except that the shallowest step was intended to pass through the scattering layer which occurred at an average depth of 28 m and 26 m, respectively. Thirteen tows on cruise N057 used a continuous oblique method by paying out and retrieving 650 m of wire for 30 minutes because of headline transducer system failure. Standard cruises used a three step oblique tow (hereafter called a standard tow) at 200, 100 and 50 m depths.

Ship's speed and tow depth were averaged from observations taken every minute during stepped oblique tows and every three minutes during horizontal tows. Observations on net mouth dimensions were made with the same frequency during tows using SCANMAR.

The net was raised, washed and picked over on the wings and body because washing was only effective for the codend and back of the belly. However, it was not possible with a net of this size to locate and remove all fang-toothed and elongate species (especially at night) which were often entangled in the net. Badly damaged animals (no skin, missing flesh, faded colours) were discarded during sorting at sea or later onshore to guard against carryover of specimens to subsequent tows. These criteria became more problematic for very deep (1000 m) tows where most of the catch was of poor quality due to the long retrieval period.

IYGPT samples were subdivided immediately into categories of fish, crustaceans, squid, and other invertebrate components and wet displacement volumes were determined for each (± 0.05 l). Samples were preserved in 10% buffered formalin. Fish samples were later sorted and individuals identified to species (or closest taxon when damaged). At least two species of *Cyclothone* (*Cyclothone braueri* and *Cyclothone microdon*) were collected but individuals were so badly damaged that they were identified only to genus. All fish were transferred to 50% isopropanol for longterm storage and archived in the Scott-Templeman Collection, Atlantic Reference Centre, St. Andrews, New Brunswick. Vertical temperature-salinity profiles were collected with a Conductivity-Temperature-Depth Probe (CTD) from the surface to a minimum of 500 m depth at the end of tows as weather permitted. Water samples were collected at maximum CTD depths with a rosette sampler to calibrate CTD salinity determinations. Expendable bathythermographs (XBT) recording to 460 or 1830 m depths were released during poor weather and at ten mile intervals along the transects. Surface temperatures and salinities were obtained by bucket at all oceanographic locations.

2.2.2 Data Analysis

Samples were pooled across cruises to determine the species composition and diversity of the mesopelagic fish fauna, after species with primarily epipelagic, bathypelagic or benthic life histories (as indicated by the authorities used to identify them) were removed. The mesopelagic fauna is therefore represented by a collection of species taken from locations with different physical characteristics, some of which were more comprehensively sampled (LSW, WSW, shallow depths) than others (GS, greater depths, Table 2.2).

The term 'species diversity' embodies two concepts: species richness, which is the number of species captured in a defined sampling unit, and species evenness, the relative abundance of the constituent species (Magurran 1988). These faunal attributes were examined separately.

Species richness was measured as the total number of species captured. Because that index is sensitive to sample size, the expected number of species for a given sample size was generated using a rarefaction curve (Hurlbert 1971). Rarefaction estimates the number of species which would be taken in a sample of **n** individuals:

$$E(S_n)=\sum\left\{1-\left[\frac{\binom{N-N_i}{N}}{\binom{N}{n}}\right]\right\}$$

where $\mathbf{E(S_n)}$ is the number of species expected to occur in a sample of a given size, **N** is the total number of individuals, **n** is the size of the sample drawn and $\mathbf{N_i}$ is the number of individuals belonging to the ith species. Species records from all surveys were pooled to obtain **N** and $\mathbf{N_i}$, using a computer program developed by Simberloff (1978) which was modified to also provide confidence limits (Heck et al. 1975). Plotting **n** against $\mathbf{E\ (S_n)}$ will result in a

Table 2.2. Numbers of midwater tows pooled by water mass, diurnal period and tow depth (total number of samples =302). Water masses are delineated by the 200 m water temperature where the sample was taken: < 9 °C = Labrador Slope Water (LSW), 9-14.9 °C = Slope Water (WSW) and ≥ 15 °C = Gulf Stream (GS); D - day, N - night.

	Water mass:	LSW		WSW		GS	
Diurnal phase	Day	21		42		5	
	Night	59		153		10	
	Sunrise	3		5		1	
	Sunset	0		3		0	
	Day/Night:	D	N	D	N	D	N
Tow depth (night and day tows only)	0-299 m	0	58	4	149	2	10
	300-699 m	10	1	13	2	3	0
	700-1001 m	11	0	25	2	0	0

flattening slope or asymptote, if sampling has been sufficient to capture most species present.

Patterns in the distribution of abundance among species were assessed by examining relative abundance and frequency of occurrence. Percent total catch by species (or evenness) was represented by a species abundance curve ((Magurran 1988) constructed by plotting the log of relative abundance against rank in order of decreasing species dominance. If only a small proportion of the species are very abundant and the majority are rare, the slope of the curve is steep. As the proportion of species with intermediate abundance increases, abundance becomes more evenly distributed and the curve appears sigmoidal.

In addition to characterising the species diversity of the whole collection, species composition and abundance (as numbers of individuals, numbers of species and volume per tow) were compared between LSW, WSW and GS sample groups based upon shallow night tows and between tow depths using WSW samples pooled into three tow depth groups. Comparisons of species composition and catch statistics were restricted to the largest sample groups (Table 2.2). Volume per tow included all species captured (both meso- and non-mesopelagic components), however, the contribution by non-mesopelagic species was assumed to be negligible because they were generally postlarvae or juveniles and, on average, constituted 1.3 % of the total number of fish captured at any site. Tow duration was considered to include both towing and haulback times, so abundance estimates were standardized to a 40 minute tow to minimize differences between horizontal and three-step tows. All estimates are calculated as geometric (or retransformed) averages of log-transformed (ln (x+1)) catches. Differences between sample groups were tested statistically using parametric analysis of variance (ANOVA). If significant differences were found, sample groups were compared on a pairwise basis using Tukey's Honestly Significant Difference (HSD) test at a significance level of 0.05. Similarities in species composition between sample groups were measured by Spearman rank correlations (**r**) of the rank order of the ten most abundant species occurring in each sample group. Species richness estimated as the total number of species captured within each water mass was not meaningful because sampling effort was too variable. Thus, species richness of a water mass was calculated as the number of species in a sample of 1000 individuals (average catch size of WSW samples) as estimated by rarefaction.

Seasonal variation in species ranking, relative abundance and numbers per tow were examined by comparisons between surveys of shallow, night samples from the WSW.

2.3 Results

2.3.1 Species composition

A total of 239,412 mesopelagic fish was captured, representing 227 species (and 26 unidentifiable taxa) in 40 families (Table 2.3). An additional 117 taxa were identified as epipelagic, bathypelagic and benthic species

Table 2.3. Percent frequency of occurrence (%FO) and total numbers (Catch) for all mesopelagic fish species captured in standard surveys (200 tows) and exploratory surveys (102 tows) and rank order of 25 most abundant species.

	Standard			**Exploratory**		
Species name	**%FO**	**Catch(Rank)**		**%FO**	**Catch(Rank)**	
Squalidae						
Squaliolus laticaudus	0	0		3	3	
Nemichthyidae						
Avocettina infans	1	2		1	1	
Nemichthys curvirostris	1	1		1	1	
Nemichthys scolopaceus	83	769	(18)	81	346	(23)
Derichthyidae						
Derichthys serpentinus	6	14		7	22	
Nessorhamphus ingolfianus	21	65		15	33	
Serrivomeridae						
Serrivomer beani	52	864	(17)	44	402	(20)
Serrivomer brevidentatus	4	8		2	3	
Eurypharyngidae						
Eurypharynx pelecanoides	11	73		19	84	
Bathylagidae						
Bathylagus berycoides	14	48		7	11	
Bathylagus compsus	24	155		22	32	
Bathylagus euryops	21	320		16	88	
Bathylagus greyae	3	9		7	12	
Bathylagus sp.	1	2		12	22	
Nansenia groenlandica	2	3		2	3	
Nansenia oblita	2	3		0	0	
Gonostomatidae						
Bonapartia pediolota	2	6		6	24	
Cyclothone sp.	17	2464	(8)	15	2018	(6)
Diplophos taenia	3	6		5	5	
Gonostoma atlanticum	5	26		0	0	
Gonostoma bathyphilum	0	0		1	1	
Gonostoma denudatum	0	0		6	8	
Gonostoma elongatum	80	1753	(11)	73	1267	(10)
Margrethia obtusirostra	6	11		15	25	
Sternotychidae						
Argyropelecus aculeatus	61	1557	(13)	58	813	(14)
Argyropelecus affinis	1	1		3	3	
Argyropelecus gigas	2	4		1	1	
Argyropelecus hemigymnus	33	207		22	56	
Argyropelecus lychnus lychnus	1	1		0	0	
Argyropelecus sladeni	7	18		1	1	
Maurolicus muelleri	29	197		40	89	
Polyipnus asteroides	21	85		8	28	
Sternoptyx diaphana	20	264		16	106	
Sternoptyx pseudobscura	2	3		1	1	
Valenciennellus tripunctulatus	22	96		16	36	

Table 2 3 cont.

	Standard			Exploratory		
Species name	**%FO**	**Catch(Rank)**		**%FO**	**Catch(Rank)**	
Photichthyidae						
Ichthyococcus ovatus	3	7		2	5	
Pollichthys mauli	12	60		17	47	
Vinciguerria attenuata	36	551	(23)	31	392	(22)
Vinciguerria nimbaria	42	493	(24)	41	336	(24)
Vinciguerria poweriae	28	231		25	161	
Chauliodontidae						
Chauliodus danae	1	1		2	7	
Chauliodus sloani	95	1742	(12)	89	1050	(13)
Stomiidae						
Macrostomias longibarbatus	1	1		0	0	
Stomias boa ferox	79	902	(16)	87	540	(18)
Stomias brevibarbatus	2	6		3	3	
Astronesthidae						
Astronesthes cyaneus	0	0		1	1	
Astronesthes cyclophotus	1	1		0	0	
Astronesthes gemmifer	0	0		2	3	
Astronesthes leucopogon	1	1		0	0	
Astronesthes micropogon	0	0		1	1	
Astronesthes niger	2	5		5	6	
Astronesthes similis	1	2		1	1	
Borostomias antarcticus	8	16		2	2	
Neonesthes capensis	0	0		1	1	
Rhadinesthes decimus	0	0		1	1	
Melanostomiidae						
Bathophilus brevis	1	1		0	0	
Bathophilus longipinnis	0	0		1	1	
Bathophilus vaillanti	2	3		2	2	
Chirostomias pliopterus	3	7		2	3	
Echiostoma barbatum	2	5		1	1	
Eustomias acinosus	1	2		0	0	
Eustomias bibulbosus	1	1		0	0	
Eustomias braueri	1	1		1	1	
Eustomias dubius	1	1		0	0	
Eustomias filifer	2	9		4	4	
Eustomias longibarba	0	0		1	1	
Eustomias macronema	1	1		0	0	
Eustomias obscurus	1	1		1	1	
Eustomias polyaster	1	1		0	0	
Eustomias schmidti	2	5		1	1	
Eustomias simplex	1	1		1	1	
Flagellostomias boureei	2	3		1	1	
Grammatostomias dentatus	1	2		0	0	
Grammatostomias flagellibarba	1	1		0	0	

Table 2.3 cont.

	Standard			Exploratory		
Species name	**%FO**	**Catch(Rank)**		**%FO**	**Catch(Rank)**	
Melanostomiidae cont.						
Leptostomias gladiator	5	11		5	6	
Leptostomias haplocaulus	1	2		0	0	
Leptostomias longibarba	2	3		1	1	
Melanostomias bartonbeanii	24	79		37	89	
Melanostomias biseriatus	0	0		1	1	
Melanostomias tentaculatus	1	2		0	0	
Melanostomias valdiviae	1	1		0	0	
Pachystomias microdon	1	2		3	3	
Photonectes braueri	0	0		1	1	
Photonectes margarita	1	2		8	9	
Malacosteidae						
Aristostomias grimaldi	1	1		0	0	
Aristostomias lunifer	1	1		0	0	
Aristostomias tittmanni	4	8		6	9	
Malacosteus niger	14	67		19	42	
Photostomias guernei	39	137		43	107	
Ultimostomias mirabilis	0	0		1	1	
Idiacanthidae						
Idiacanthus fasciola	4	8		9	15	
Scopelarchidae						
Benthalbella infans	1	1		1	1	
Scopelarchus analis	4	8		1	1	
Scopelarchus michaelsarsi	2	4		0	0	
Paralepididae						
Lestidiops affinis	16	139		24	86	
Lestidiops jayakari	1	3		4	9	
Lestidium atlanticum	2	7		5	5	
Lestrolepis intermedia	2	4		6	13	
Macroparalepis affine	11	85		4	4	
Notolepis rissoi	80	3442	(6)	82	1527	(7)
Paralepis atlantica	5	126		9	22	
Paralepis brevirostris	3	14		5	17	
Paralepis coregonoides	1	6		0	0	
Paralepis elongata	0	0		1	1	
Stemonosudis intermedia	2	3		4	8	
Sudis hyalina	10	28		22	25	
Uncisudis longirostris	3	17		2	3	
Evermanellidae						
Coccorella atlantica	7	17		7	13	
Evermanella balbo	19	64		28	57	
Evermanella indica	7	26		4	5	
Omosudidae						
Omosudis lowei	0	0		1	1	

Table 2.3 cont.

	Standard			Exploratory		
Species name	**%FO**	**Catch(Rank)**		**%FO**	**Catch(Rank)**	
Myctophidae						
Benthosema glaciale	90	45279	(2)	78	13882	(3)
Benthosema suborbitale	12	87		19	67	
Bolinichthys indicus	31	675	(21)	35	167	
Bolinichthys photothorax	2	3		8	10	
Bolinichthys supralateralis	12	39		3	4	
Centrobranchus nigro-ocellatus	1	1		0	0	
Ceratoscopelus maderensis	94	46547	(1)	100	24928	(1)
Ceratoscopelus warmingii	45	2564	(7)	36	1169	(11)
Diaphus bertelseni	2	7		6	7	
Diaphus brachycephalus	11	33		8	15	
Diaphus dumerilii	60	956	(15)	45	393	(21)
Diaphus effulgens	19	110		17	77	
Diaphus fragilis	1	4		0	0	
Diaphus garmani	0	0		1	3	
Diaphus holti	0	0		1	4	
Diaphus lucidus	13	58		20	54	
Diaphus luetkeni	0	0		1	1	
Diaphus metopoclampus	10	23		14	39	
Diaphus mollis	28	703	(20)	22	157	
Diaphus perspicillatus	13	204		16	136	
Diaphus rafinesquii	37	346		42	291	(25)
Diaphus roei	1	1		0	0	
Diaphus splendidus	6	22		9	13	
Diaphus termophilus	1	2		1	1	
Diogenichthys atlanticus	5	23		5	13	
Electrona rissoi	0	0		1	1	
Gonichthys cocco	2	3		3	3	
Hygophum benoiti	48	2424	(9)	34	1136	(12)
Hygophum hygomii	44	8436	(4)	58	2477	(5)
Hygophum macrochir	1	2		0	0	
Hygophum reinhardtii	13	52		9	15	
Hygophum taaningi	6	30		5	6	
Lampadena anomala	3	7		2	2	
Lampadena atlantica	10	43		18	26	
Lampadena chavesi	3	6		6	10	
Lampadena luminosa	4	10		3	3	
Lampadena speculigera	28	125		28	78	
Lampanyctus alatus	55	233		28	75	
Lampanyctus ater	40	264		44	239	
Lampanyctus crocodilus	65	655	(22)	55	631	(16)
Lampanyctus cuprarius	1	1		7	11	
Lampanyctus festivus	12	60		8	14	
Lampanyctus intricarius	1	1		7	11	

Table 2.3 cont.

	Standard			Exploratory		
Species name	**%FO**	**Catch(Rank)**		**%FO**	**Catch(Rank)**	
Myctophidae cont.						
Lampanyctus lineatus	26	128		16	73	
Lampanyctus macdonaldi	9	85		6	14	
Lampanyctus nobilis	3	15		1	1	
Lampanyctus photonotus	34	322		35	242	
Lampanyctus pusillus	51	1037	(14)	53	683	(15)
Lepidophanes gaussi	5	50		7	81	
Lepidophanes guentheri	53	2130	(10)	49	1277	(9)
Lobianchia dofleini	70	18665	(3)	75	14912	(2)
Lobianchia gemellerii	44	728	(19)	43	581	(17)
Loweina rara	5	11		1	1	
Myctophum affine	18	123		9	67	
Myctophum asperum	1	3		0	0	
Myctophum nitidulum	2	4		1	1	
Myctophum obtusirostre	1	1		1	1	
Myctophum punctatum	49	425	(25)	51	1398	(8)
Myctophum selenops	14	72		24	111	
Notolychnus valdiviae	1	1		0	0	
Notoscopelus bolini	4	8		4	4	
Notoscopelus caudispinosus	24	362		25	213	
Notoscopelus elongatus	6	74		25	447	(19)
Notoscopelus resplendens	65	4660	(5)	61	3310	(4)
Protomyctophum arcticum	9	59		3	11	
Symbolophorus veranyi	32	213		34	116	
Taaningichthys bathyphilus	4	11		8	11	
Taaningichthys minimus	1	4		3	3	
Gadidae						
Micromesistius poutassou	1	1		0	0	
Melanonidae						
Melanonus zugmayeri	12	38		16	28	
Trachipteridae						
Zu cristatus	1	2		3	3	
Regalecidae						
Regalecus glesne	1	2		3	3	
Stylephoridae						
Stylephorus chordatus	0	0		3	3	
Diretmidae						
Diretmus argenteus	5	14		5	9	
Anoplogasteridae						
Anoplogaster cornuta	8	22		9	11	
Melamphaeidae						
Melamphaes eulepis	2	4		0	0	
Melamphaes longivelis	1	1		0	0	
Melamphaes polylepis	1	1		0	0	

Table 2.3 cont.

Species name	Standard %FO	Standard Catch(Rank)	Exploratory %FO	Exploratory Catch(Rank)
Melamphaidae cont.				
Melamphaes suborbitalis	12	37	24	62
Melamphaes typhlops	12	119	6	21
Poromitra capito	16	67	20	34
Poromitra megalops	2	3	1	1
Scopeloberyx opisthopterus	8	82	14	75
Scopeloberyx robustus	0	0	3	22
Scopelogadus beanii	18	307	17	192
Scopelogadus mizolepis	3	15	12	112
Rondeletiidae				
Rondeletia loricata	3	7	4	5
Zeniontidae				
Zenion hololepis	1	1	0	0
Zeidae				
Cyttopsis roseus	1	1	0	0
Grammicolepidae				
Daramattus americanus	1	1	1	1
Caproidae				
Antigonia spp.	4	9	9	12
Liparidae				
Paraliparis calidus	0	0	1	2
Apogonidae				
Epigonus pandionis	0	0	1	1
Epigonus telescopus	1	1	1	1
Percichthyidae				
Howella sherborni	41	242	51	151
Synagrops bellus	7	20	11	23
Synagrops spinosa	3	6	7	10
Bramiidae				
Pterycombus brama	6	12	5	5
Caristiidae				
Caristius groenlandicus	3	5	2	2
Chiasmodontidae				
Chiasmodon sp.	14	50	29	66
Pseudoscopelus altipinnus	11	22	8	9
Scombrolabracidae				
Scombrolabrax heterolepis	0	0	2	2
Gempylidae				
Diplospinus multistriatus	5	13	21	46
Gempylus serpens	1	1	0	0
Nealotus tripes	20	128	26	119
Neopinnula orientalis	0	0	1	1
Nesiarchus nasutus	1	2	2	2

Table 2.3 cont.

Species name	**Standard** %FO	Catch(Rank)	**Exploratory** %FO	Catch(Rank)
Trichiuridae				
Aphanopus carbo	3	5	1	1
Benthodesmus elongatus simonyi	13	58	15	27
Stromateidae				
Centrolophus medusophagus	1	2	0	0
Centrolophus niger	0	0	2	2
Cubiceps gracilis	3	5	6	16
Cubiceps pauciradiatus	6	21	19	42
Psenes maculatus	4	10	11	18
Psenes pellucidus	2	4	5	6
Ariomma sp.	11	70	13	33

(Appendix 1). The most abundant mesopelagic fish families were Myctophidae (87% of the total catch), Gonostomatidae (3.2%), Paralepididae (2.4%) and Sternoptychidae (1.5%). Myctophidae was also the most speciose family with 68 species followed by Melanostomiidae (31 species), Paralepididae (13 species) and Sternoptychidae (11 species) (some Gonostomatidae were not identified to species level).

The lack of an asymptote in the rarefaction curve (Fig. 2.2) indicates that the fauna was insufficiently sampled for the collections to represent all the mesopelagic species occurring in the Slope Sea (Simberloff 1978). It is due to the large proportion of rare species; twenty-two percent of all species records were based upon single captures and a few new records were discovered with each additional survey. The pattern in relative abundance was that few species were very abundant or occurred frequently, while a large number were rare. Three myctophids, *Ceratoscopelus maderensis, Benthosema glaciale* and *Lobianchia dofleini,* comprised 70% of all individuals captured and twelve species were captured in numbers exceeding 1% of the pooled catch (Table 2.3, Fig. 2.3a). Only seven species occurred in more than 75 % of all tows, and 80% of all species occurred in fewer than 20% of the samples (Fig. 2.3b). However, the species abundance curve (Fig. 2.3c) appears slightly concave indicating the presence of species with intermediate abundance. A semi-logarithmic plot of species abundance illustrates the relative size of the abundance classes. Although the modes representing rare and very abundant

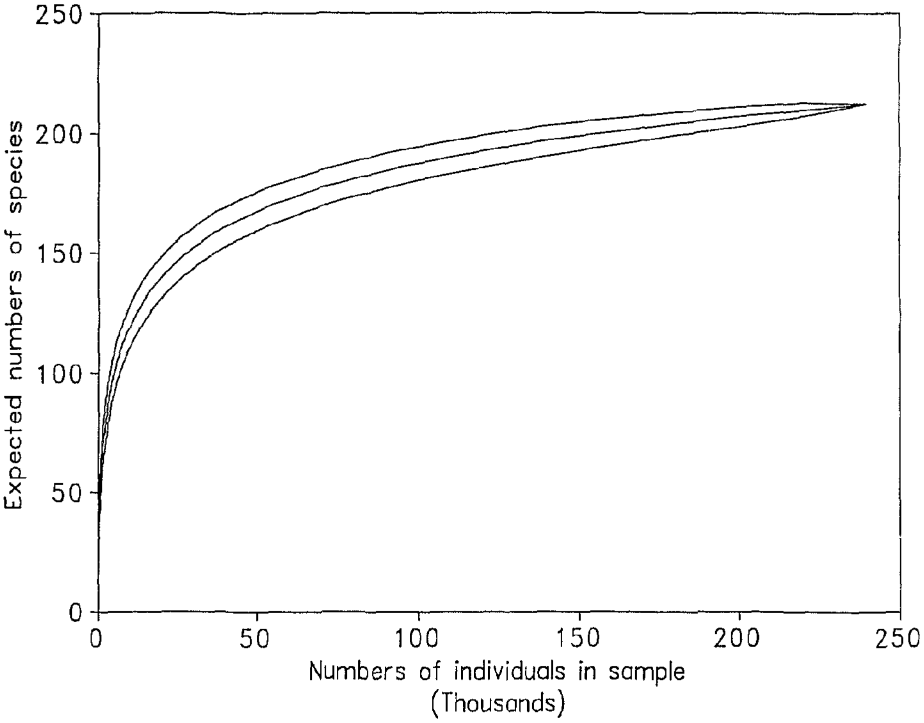


Figure 2.2. Expected number of mesopelagic fish species in relation to increasing sample size in the Slope Sea (central line). Upper and lower lines indicate the 95% confidence limits for the curve.

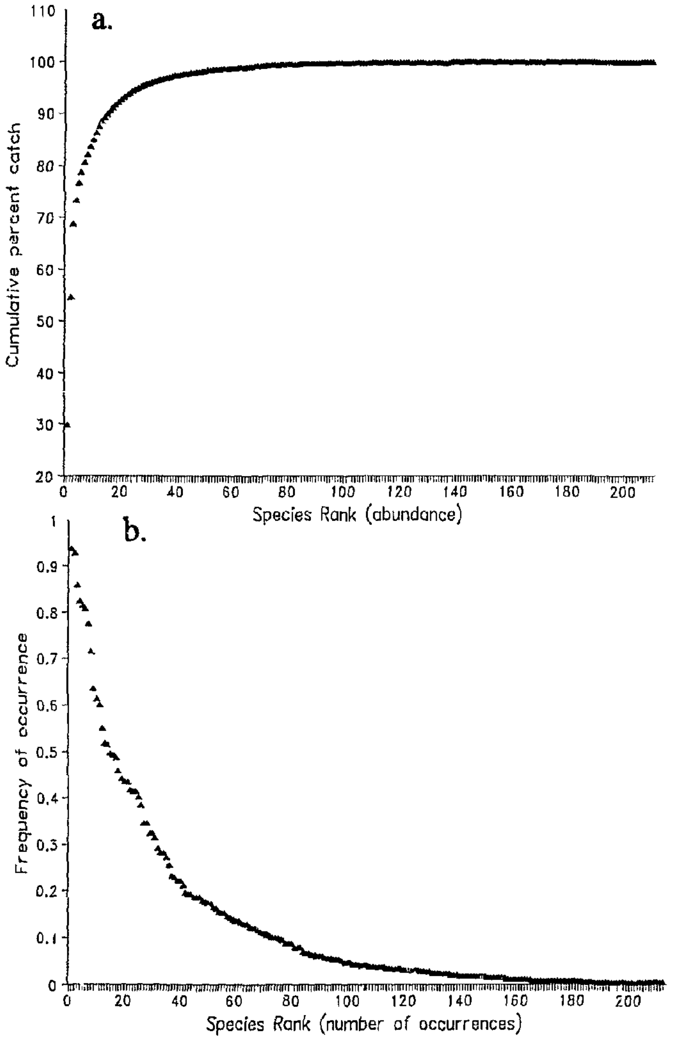
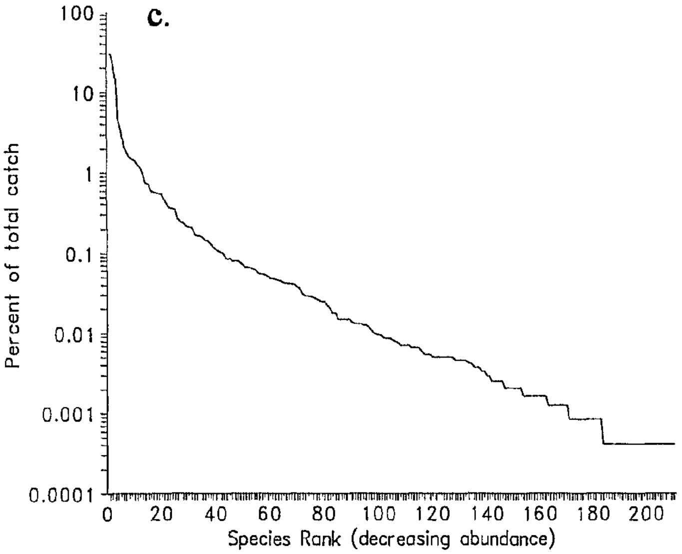


Figure 2.3. Diversity of the mesopelagic fish fauna of the Slope Sea. Cumulative percent total catch (numbers) by species ranked in decreasing order of abundance; b. Frequency of occurrence of species ranked in order of decreasing abundance;



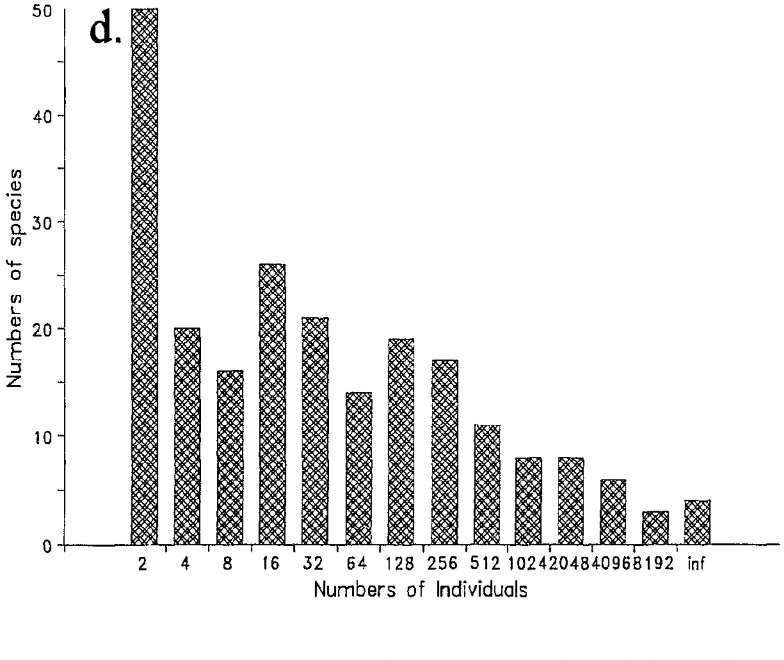


Figure 2.3 cont: c. Percent contribution to total catch by each species ranked in order of decreasing abundance; d. Abundance distribution of all species.

species are conspicuous, there is also a group of species with intermediate abundance or common abundance (Fig 2.3d).

2.3.2 Factors correlating with variations in species composition and abundance

Towing depth: Mean number of fish per tow, species per tow, and volume per tow of samples collected in WSW differed significantly between depths (ANOVA, $p < 0.01$, Table 2.4). Shallow tows caught the most animals, followed by deep tows (Tukey HSD test, $p<0.05$). Shallow and deep tows caught more species per tow than mid-depth tows and tow volume was highest in the deepest sample group (Tukey, $p<0.05$). Rank order of the ten most abundant species were significantly correlated between mid-depth and deep tows, but not shallow tows (Spearman, $p=0.05$, Table 2.5). Myctophids did not dominate deep tows to the same extent as shallower tows. Three myctophids ranked among the top ten species in tows between 700-1000 m as compared to eight in shallow tows. *Benthosema glaciale* shifted from third to first in rank with increasing tow depth. *Cyclothone* spp., the second most abundant species in deep tows, was captured in only five shallow tows. Similarity in rank order between abundant species in shallow tows (Table 2.5) and the combined collections (Table 2.3) demonstrates the influence of the sampling design on the apparent relative abundance of individual species.

Table 2.4. Geometric mean numbers of individuals, species and volume (l) per 40 minute IYGPT tow in warm Slope Water (WSW) samples pooled by tow depth (volume includes non-mesopelagic species). Parametric ANOVA was used to determine if differences between means were significant at $p < 0.05$.

	Depth (m)			
	0-299	300-699	700-1001	sig.
No. of species	214	103	144	
numbers/tow	613.4	191.5	339.3	$p < 0.001$
no. of tows	153	15	27	
numbers of species/tow	29.4	19.9	27.1	$p < 0.01$
no. of tows	153	15	27	
vol/tow (l)	0.8	0.7	1.86	$p < 0.001$
no. of tows	145	14	26	

Table 2.5. Rank order of the ten most abundant species collected in Warm Slope Water tows pooled by tow depth, and Spearman rank correlation coefficients (r). * - r significant at p=0.05.

Species Name	0-299 m	300-699 m	700-1000 m
Benthosema glaciale	3	2	1
Cyclothone spp.	(29)	(11.5)	2
Ceratoscopelus maderensis	1	1	3
Chauliodus sloani	(12)	5	4
Serrivomer beani	(36)	6	5
Lobianchia dofleini	2	4	6
Stomias boa	(20)	(11.5)	7
Gonostoma elongatum	10	7	8
Scopelogadus beanii	(51)	(29)	9
Notolepis rissoi	6	10	10
Notoscopelus resplendens	5	(19)	(11)
Sternoptyx diaphana	(102.5)	8	(13)
Hygophum hygomii	4	3	(15)
Argyropelecus aculeatus	11	9	(17)
Hygophum benoiti	7	(17)	(23)
Lepidophanes guentheri	9	(13)	(24)
Ceratoscopelus warmingii	8	(90)	(31.5)

Spearman r	0-299m	300-699m	700-1000m
0-299 m	1.0		
300-699 m	0.326	1.0	
700-1000m	0.07	0.607*	1.0

Water mass: Mean number of fish per tow and number of species per tow differed significantly between LSW, WSW and GS (ANOVA, $p=0.02$, Table 2.6) while differences in mean volume per tow were not significant ($p=0.11$, Table 2.6). Mean number of fish per tow in the WSW was significantly higher than in the LSW (Tukey, $p<0.05$) but the numbers per tow in the GS, and WSW or LSW were not significantly different. Mean number of species per tow was highest in GS samples, followed by WSW tows (Tukey, $p<0.05$). All unique species records in LSW and GS samples are from single occurrences (only one specimen of each species was captured) while unique species records in WSW samples included one to twenty individuals. Of 227 species captured, 63 (28% of total) occurred in all three sample groups. LSW and WSW samples shared 30 species (13%) not found in GS: LSW and GS shared one species (< 1%): and 45 species (20%) occurred in WSW and GS but not LSW.

Rarefaction curves were used to compare species richness between water masses (Fig. 2.4). Confidence intervals about the three lines do not overlap at levels of 1000 or more individuals. The GS had the highest richness ($(E(S))_{1000} = 73.7$), followed by WSW ($(E(S))_{1000} = 51.7$) and LSW ($(E(S))_{1000} = 30.6$). Although species accumulation slowed considerably at > 1000 individuals, none of the curves reached an asymptote.

The three most abundant species by water mass and percent contribution to the pooled catch were: *B. glaciale* in LSW (73.5), *C. maderensis* in WSW (38.9) and *Hygophum hygomii* in GS samples (9.8). Rank orders of the

Table 2.6. Geometric mean numbers of individuals, species and volume (l) per 40 minute IYGPT tow in Labrador Slope Water (LSW), Warm Slope Water (WSW) and Gulf Stream (GS) water masses. Samples were collected from 0-300 m depths at night. Volume includes non-mesopelagic species. Parametric ANOVA was used to determine whether differences between means were significant at $p<0.05$.

	LSW	WSW	GS	sig.
No. of species	102	214	123	
numbers/tow	415.7	643.4	475.5	$p = 0.02$
no. of tows	58	149	10	
numbers of species/tow	14.5	30.2	42.1	$p < 0.001$
no. of tows	58	149	10	
vol/tow (l)	0.6	0.8	0.7	$p = 0.11$
no. of tows	55	142	10	

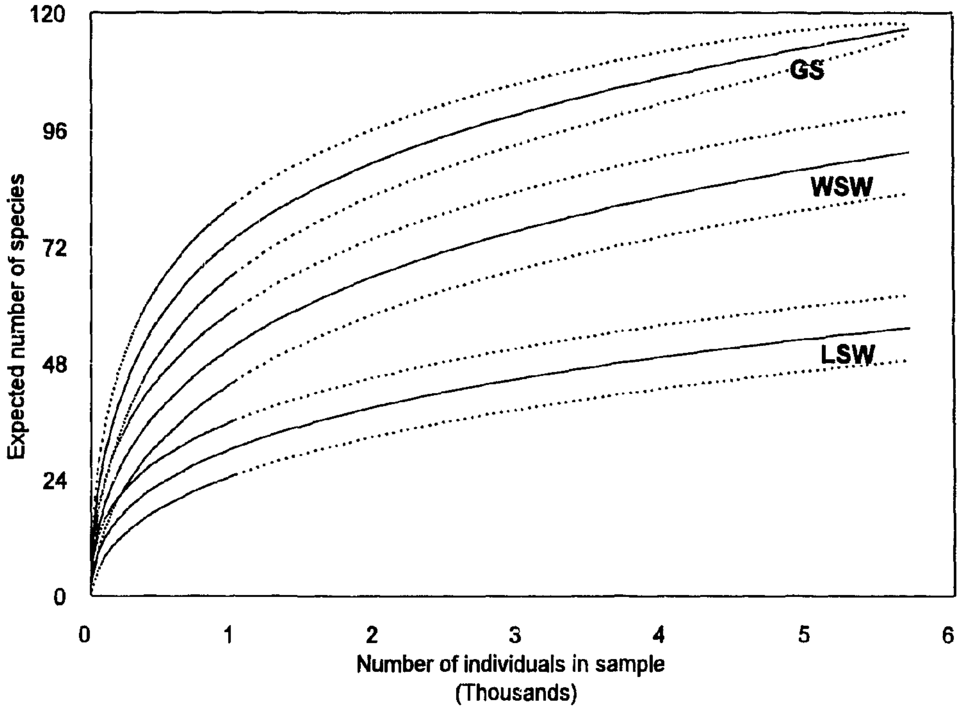


Figure 2.4. Expected numbers of species against increasing sample size in the Gulf Stream (GS), Warm Slope Water (WSW) and Labrador Slope Water (LSW) generated using rarefaction. Dotted lines indicate upper and lower 95% confidence limits for the three curves.

Table 2.7. Rank order of the ten most abundant species captured in 222 shallow night tows pooled by 200 m depth temperatures into Labrador Slope (LSW), Warm Slope (WSW) and Gulf Stream (GS), and Spearman rank correlation coefficients (r). * - r significant at p=0.05.

Species Name	LSW	WSW	GS
Benthosema glaciale	1	3	(47)
Ceratoscopelus maderensis	2	1	10
Notolepis rissoi	3	6	(77)
Myctophum punctatum	4	(21)	(22)
Lobianchia dofleini	5	2	2
Notoscopelus resplendens	6	5	6
Hygophum hygomii	7	4	1
Notoscopelus elongatus	8	(57)	(108)
Stomias boa	9	(20)	(64)
Chauliodus sloani	10	(13)	(29.5)
Hygophum benoiti	(13)	8	9
Gonostoma elongatum	(17)	10	(12)
Ceratoscopelus warmingii	(18)	7	3
Lepidophanes guentheri	(20.5)	9	7
Bolinichthys indicus	(28)	(23)	5
Lampanyctus photonotus	(37.5)	(30)	8
Diaphus mollis	(48)	(24)	4

Spearman r	LSW	WSW	GS
LSW	1.0		
WSW	0.65*	1.0	
GS	-0.38	0.25	1.0

ten most abundant species in each sample group are shown in Table 2.7. Four species ranked among the top ten in all three regions. Two species, *B. glaciale* and *Notolepis rissoi* (or *Arctozenus rissoi,* see Post 1988), were among the top ten in both the LSW and WSW, and three species, *Hygophum benoiti, Ceratoscopelus warmingii* (or *C. townsendi,* see Badcock and Araujo 1988) and *Lepidophanes guentheri,* were highly ranked in both the WSW and GS. No species abundant in one area was absent from another, and species such as *L. dofleini* and *Notoscopelus resplendens* had similar ranks in all regions. Some species showed striking changes in ranking, e.g., *B. glaciale* and *N. rissoi* which ranked first and third in LSW, ranked 47 and 77, respectively, in the GS. Conversely, *C. warmingii* and *Diaphus mollis* are ranked third and fourth in the GS, and 18 and 48, respectively, in the LSW. Species composition was correlated between LSW and WSW sample groups (Spearman, p=0.05, Table 2.7).

Season: Spearman rank correlation coefficients indicate significant correlation in species composition in WSW among most cruises (p=0.05, Table 2.8). However, February cruises (N057, N096) were weakly correlated with each other and the December survey (N112) only. Species composition differed from the other surveys due to lower ranking (greater relative abundance) of *N. rissoi, Stomias boa, Myctophum punctatum* and *H. benoiti,* and higher ranking of species such as *L. dofleini, C. warmingii, L. guentheri* and *H. hygomii.* Lack of correlation between December (N112) and both June (N122) and Sept (N089),

Table 2.8. Spearman rank correlation coefficients for ranks of top 10 species in shallow (0-299 m), nighttime Warm Slope Water tows pooled by survey. Shading indicates coefficients not significant at P > 0.95.

	Dec (N112)	Feb (N057)	Feb (N096)	Apr (N119)	June (N122)	Aug (N067)	Aug (N126)	Sept (N089)	Oct (H127)	Oct N110)
Dec (N112)	1.000									
Feb (N057)	0.476	1.000								
Feb (N096)	0.379	0.455	1 000							
Apr (N119)	0.545	0.197	0.443	1.000						
Jun (N122)	0.370	-0.025	0.077	0.661	1 000					
Aug (N067)	0.450	0.008	0.228	0.670	0.834	1.000				
Aug (N126)	0.481	-0.119	-0.024	0.662	0.902	0.901	1.000			
Sep (N089)	0.404	-0.172	-0.124	0.366	0.659	0.669	0.812	1.000		
Oct (H127)	0 839	0.393	0.367	0.585	0.491	0.563	0.577	0.477	1.000	
Oct (N110)	0.694	0.096	0.202	0.774	0 782	0 865	0.913	0.695	0.744	1 000

and between April (N119) and Sept (N089) stem from a greater relative abundance of *H. benoiti* and *B. glaciale* in December and April, and lower relative abundance of *H. hygomii* (Table 2.9). Contribution to the total catch by the five most abundant species on each cruise varies with each species predominating in one or a few adjacent cruises and then declining in relative abundance (Table 2.9). *Ceratoscopelus maderensis*, the most abundant species in cruises from September to February, is superseded by *B. glaciale* in April, *H. hygomii* in June, and *L. dofleini* in August. *Hygophum benoiti* and *H. hygomii* are almost opposite in relative abundance, the former peaking in February and the latter most abundant in June. Catches in February were dominated by *C. maderensis* and *B. glaciale* whereas June and August cruises displayed a more equitable species composition which included *L. dofleini* and *H. hygomii* (Table 2.9). The percentage catch represented by the five most highly ranked species is consistently large, ranging from 67% in August (N067) to 89% in April (N119). Contribution by the first ranked species varies greatly, from as low as 22% in June (*H. hygomii;* N122) to 70% in April (*B. glaciale;* N119).

Catch rates were calculated for the individual species to see if shifts in relative abundance were due to declines in the most abundant species, or increased abundance of less important species (Table 2.10). These catch rates are variable but the patterns are very similar to those described for relative abundance. *Benthosema glaciale* declined from its April peak abundance

Table 2.9. Percent numerical contribution by abundant species to shallow (0-299 m) night-time samples in Warm Slope Water samples pooled by survey and ranking (in parentheses) of the five most abundant species in each survey, geometric mean numbers of fish and mean number of species per tow. Dash - contribution of <1% of total catch.

Species Name	Cruise Date									
	Dec (N112)	Feb (N057)	Feb (N096)	Apr (N119)	June (N122)	Aug (N067)	Aug (N126)	Sept (N089)	Oct (H127)	Oct N110)
C. maderensis	69 (1)	48 (1)	40 (2)	13 (2)	12 (3)	20 (2)	13 (3)	34 (1)	54 (1)	43 (1)
L.dofleini	12 (2)	2	-	1 (5)	21 (2)	24 (1)	33 (1)	30 (2)	29 (2)	20 (2)
B.glaciale	2 (4)	11 (3)	41 (1)	70 (1)	8 (5)	8 (3)	8 (5)	-	1	4 (5)
N.resplendens	1	-	-	-	4	8 (4)	9 (4)	10 (3)	2 (3)	6 (3)
C.warmingii	1 (5)	-	-	1	2	2	3	2	1	4 (4)
L.guentheri	1	2	-	1	2	2	3	1	2 (4)	2
N. rissoi	1	1	1 (5)	1 (4)	9 (4)	5	2	-	-	2
H. hygomii	-	-	-	4 (3)	22 (1)	7 (5)	17 (2)	5 (4)	1	2
H. benoiti	3 (3)	13 (2)	5 (3)	1	-	-	-	-	1 (5)	1
G. elongatum	1	2 (5)	1 (4)	-	3	3	1	1	1	2
L. crocodilus	1	1	-	-	-	-	-	3 (5)	-	1
V. attenuata	1	3 (4)	1	-	-	-	-	-	-	-
No. of tows	23	9	20	9	10	17	15	11	7	26
numbers/tow	805.2	276.0	449.6	904.6	1100.3	598.5	1117.9	933.7	2029.1	396.7
No. species/tow	36.1	23.4	25.1	31.2	39.8	31.5	37.3	35.7	45.3	30.9

Table 2.10. Geometric mean numbers per tow for abundant species captured in shallow, night Warm Slope Water tows using a 40 minute IYGPT tow.

Species Name	Cruise Date									
	Dec (N112)	Feb (N057)	Feb (N096)	Apr (N119)	June (N122)	Aug (N067)	Aug (N126)	Sept (N089)	Oct (H127)	Oct (N110)
C. maderensis	279.2	86.9	37.5	93.1	80.0	89.9	93.1	143.4	905.5	88.3
L. dofleini	73.3	2.7	1.6	5.4	173.3	57.9	216.9	200.2	375.4	47.1
B. glaciale	10.7	33.1	168.7	447.2	66.1	15.0	36.1	2.3	3.8	6.3
N. resplendens	7.8	1.4	2.4	4.3	29.7	23.2	61.0	45.8	24.7	11.8
C. warmingii	8.3	1.2	1.6	4.1	10.0	4.6	15.5	3.4	4.4	4.7
L. guentheri	9.8	3.6	1.8	9.0	12.0	6.1	11.2	5.4	17.9	4.3
N. rissoi	3.6	2.9	4.8	8.6	63.7	21.4	15.5	4.8	2.2	5.6
H. hygomii	1.4	1.0	1.8	17.7	128.2	18.8	149.2	25.0	5.2	3.8
H. benoiti	21.4	18.4	3.0	7.3	1.2	1.0	1.1	1.0	18.4	3.0
G. elongatum	9.6	6.2	4.9	4.2	18.1	6.8	11.8	7.5	13.1	4.5
L. crocodilus	7.5	3.2	2.3	2.3	1.3	2.1	2.4	16.5	5.6	3.0
V. attenuata	4.8	9.7	2.1	1.7	1.9	1.1	1.1	1.7	10.6	1.3

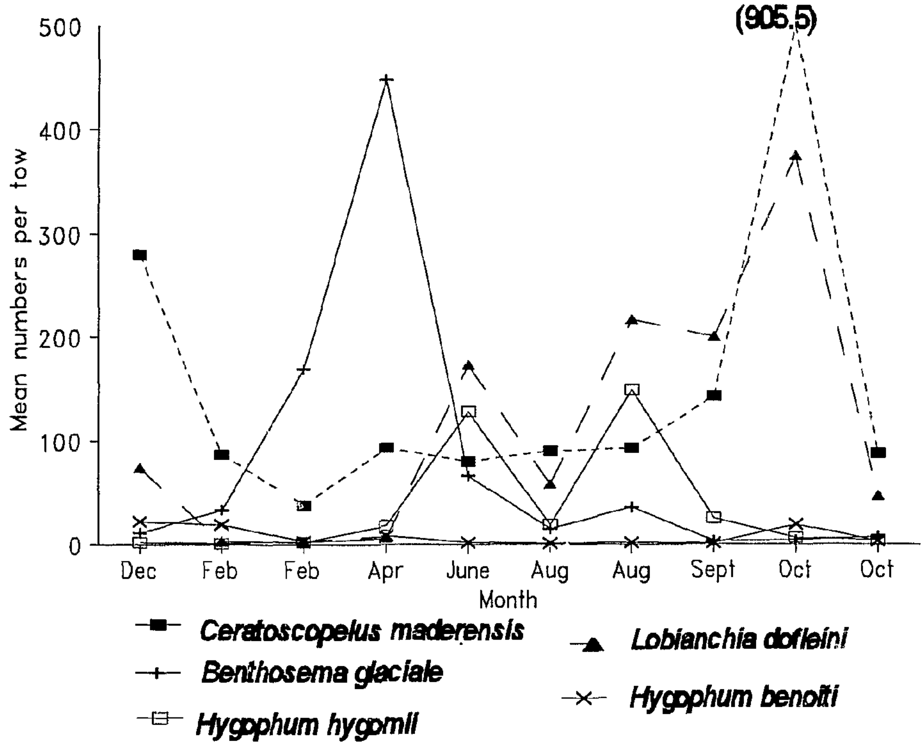


Figure 2.5. Geometric mean numbers per tow by month of abundant mesopelagic species captured by IYGPT in the Warm Slope Water.

through the summer and fall cruises. *Lobianchia dofleini* peaked in June through December and was almost absent in February (Fig. 2.5).

Comparisons of mean abundance of the nine most abundant species between winter-spring and summer-fall surveys within the same year indicate that the trends (increase or decrease) were consistent for three years (Fig 2.6). *Benthosema glaciale* and *H. benoiti* always decreased in abundance in numbers while the other seven species increased between the same surveys. The two exceptions were *C. maderensis* and *H. benoiti* whose mean abundance did not change between surveys in 1989 and 1988, respectively (Three species listed in Table 2.9 were excluded from Figure 2.6: *Vinciguerria attentuata* and *L. crocodilus* due to their low relative abundance (Table 2.9), and *G. elongatum* which showed no change in 1986 and 1988, and increased between the April and August surveys in 1989).

Overall, mean numbers of fish and species per tow varied among surveys from 276.0 to 2029.1 and 23.4 to 45.3, respectively (Table 2.9). Mean numbers of fish per tow differed significantly among cruises (ANOVA, F= 4.86, $p<0.01$), as did the numbers of species per tow (ANOVA, F= 4.21, $p<0.01$). However, few pairwise comparisons of these means were significant (Tukey, $p<0.05$, Table 2.11). Variability in these statistics is due partially to interannual variation in the abundance of individual species, such as has been observed for *B. glaciale* (Sameoto 1982, 1988). Variability in numbers of individuals and species per tow can also be attributed to differences in location

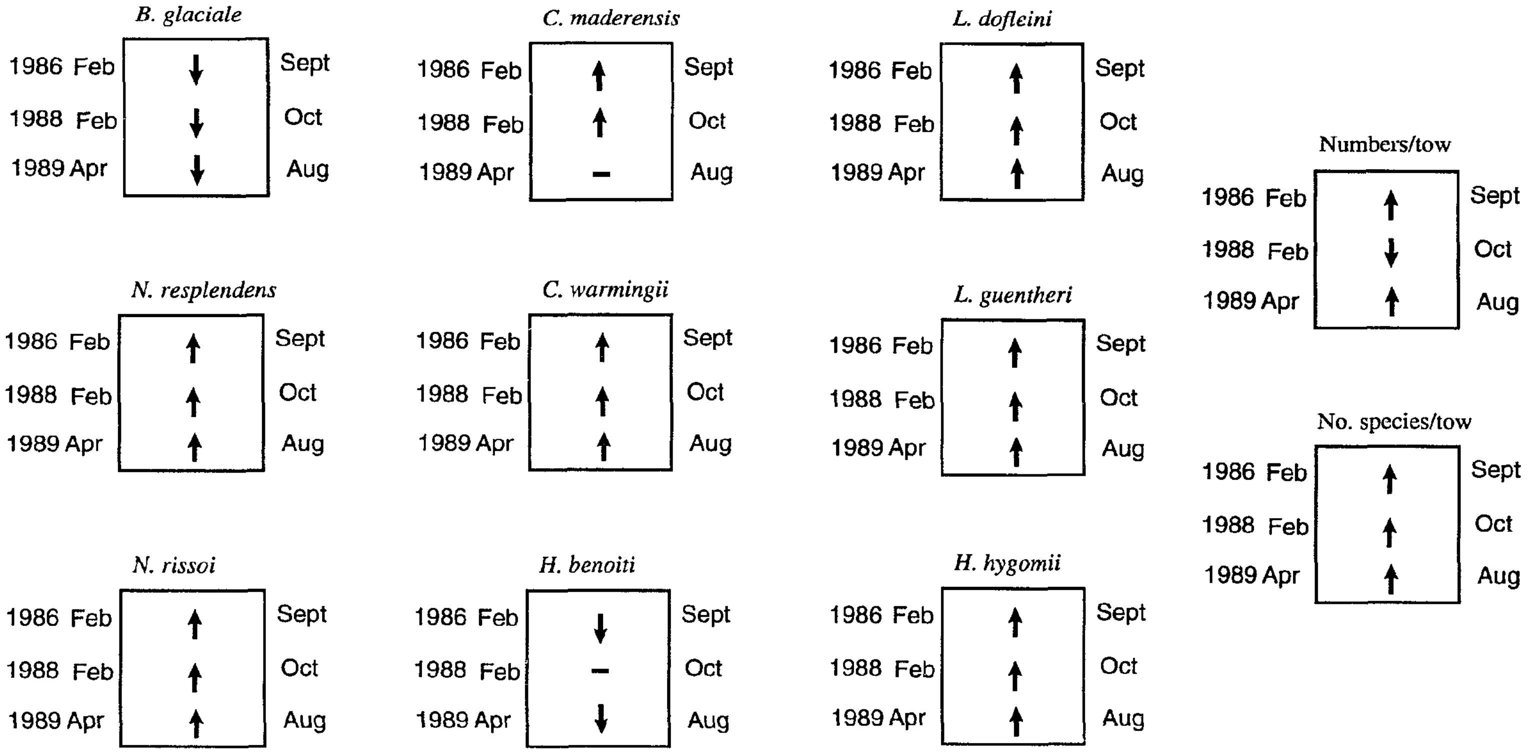


Figure 2.6. Direction of change in mean abundance between cruise pairs in 1986, 1988 and 1989 (↑ increase, ↓ decrease, – no change).

Table 2.11 Comparison of numbers per tow (above diagonal) and numbers of species per tow (below diagonal) in WSW surveys by Tukey HSD test. Values differing at p<0.05 are shown.

		Number of fish per tow									
		June	Feb	Feb	Apr	June	Aug	Aug	Sept	Oct	Oct
		N112	N057	N096	N119	N122	N067	N126	N089	H127	N110
	N112		0.05	-	-	-	-	-	-	-	-
	N057	0.05		-	-	0.05	-	0.05	0.05	0.05	-
Number	N096	-	-		-	-	-	-	-	0.05	-
of	N119	-	-	-		-	-	-	-	-	-
species	N122	-	0.05	0.05	-		-	-	-	-	-
per	N067	-	-	-	-	-		-	-	-	-
tow	N126	-	0.05	-	-	-	-		-	-	0.05
	N089	-	-	-	-	-	-	-		-	-
	H127	-	0.05	0.05	-	-	-	-	-		0.05
	N110	-	-	-	-	-	-	-	-	-	

and sampling methods between the exploratory and standard cruises. Cruise H127 stands out in terms of rather anomalous catches of C. *maderensis, L. dofleini, H. benoiti* and *Vinciguerria attenuata* (Table 2.10) because catch rates were significantly different from the other October cruise (N110), and because species richness was higher than any other cruise. Cruise H127 was the only one in which the third IYGPT step was towed at about 25 m depth through the scattering layer, rather than at 50 m as in the standard cruises such as N110. The shallower step may be more effective in catching animals overall, though species richness and rank order are not greatly different.

2.4 Discussion

2.4.1 Species composition

The mesopelagic fish fauna in the Canadian Atlantic region is more diverse than previously realized. Ninety of 227 species (about 40% of the species identified) are new records for this region of the Atlantic. Most represent northern extensions of distributions associated with the Sargasso or Caribbean Seas (e.g. Morrow and Gibbs 1964, Nafpaktitis et al. 1977, Backus *et al.* 1970, 1977; Gartner et al. 1987, 1989; Karnella 1987). The large faunal list is due partially to the higher frequency of sampling than earlier efforts of 24 to 65 tows (Jahn and Backus 1976; Backus and Craddock 1982; McKelvie 1985a). Relatively larger filtering volumes (Kashkin and Parin 1983) probably also contributed to greater observed species richness. The mouth area of the IYGPT is about ten times larger than that of the midwater trawl used by Backus and co-workers. Previous investigations deploying large trawls also reported an increase in species richness, e.g. McKelvie (1985a) reported 168 species in 65 tows using an Engels Midwater Trawl which had a mouth area six times that of the IYGPT.

A salient feature of the results from the rarefaction curve was that it indicated an insufficiently sampled fauna, in spite of high sampling intensity and high number of new records. Perhaps more sampling is required before reliable conclusions can be made about the faunal composition of the Slope Sea. However, evidence suggests that the sampling design violated the underlying assumption of the model, causing it to overestimate the numbers of species present. These assumptions were that the abundance of any species in the collection was proportional to its abundance in the environment and that the animals were randomly distributed.

The estimate of the total number of species was influenced by the high percentage of species occurring only once to a few times in the collection. Some of these were ecologically rare species which would seldom be captured regardless of sampling intensity, others might appear rare because they were expatriated from regions outside the study area, or because their preferred environment was poorly sampled. An examination of the status of the 50 species which only occurred once or twice (Table 2.3) indicates that only a portion of these are genuinely rare. Based upon published descriptions of their geographic range and life history, almost 40 of these species may have been undersampled because they normally occur in a habitat which was poorly sampled or because they were likely to have been expatriated from other regions. These are species which exhibit a distribution of abundance at night which is closely associated with the surface (e.g., *Centrobranchus ocellatus, Myctophum obtusirostre*; Karnella 1987, Nafpaktitis et al. 1977), are bathypelagic as adults (melamphaids, omosudids and scopelarchids; Ebeling and Weed 1973; Post 1984; Johnson 1984) or species expatriated from the Eastern Atlantic (*Diaphus holti, Electrona risso*) and Caribbean and Sargasso Seas (*Nemichthys curvirostris*, some *Eustomias* species, *Diaphus luetkeni, Hygophum macrochir*; Nafpaktitis et al. 1977)). Abundance of species with a small average adult size, such as *Notolychnus valdiviae* and *Diogenichthys atlanticus*, may be underestimated since the IYGPT does not effectively sample animals less than 25 mm in length (the minimum size of 95% of all species lots was greater than 19 mm). However, it is unlikely that large populations of these species were overlooked, since they were also uncommon in Slope Water samples examined by Nafpaktitis et al. 1977. The effect of the lower size limit catchable by the IYGPT should have been offset by the bimonthly sampling. Most mesopelagic species, other than *Cyclothone* spp., grow large enough over the year to be captured in one or more surveys. The remaining ten very uncommon species are truly rare, based upon their frequency of capture in other distributional studies (Morrow 1964; Morrow and Gibbs 1964).

Rarefaction will also overestimate species richness when samples are not distributed randomly (as in this study), or if the data used to generate the expected number of species curve includes species with aggregated distributions (Krebs 1989). Observations from submersibles on mesopelagic fishes in the Slope Water, as well as catch data from surveys in several regions indicate aggregated distributions of myctophids (Backus et al. 1968; Jahn 1976; Barnett 1983; Karnella 1987; Auster et al. 1992). When actual species counts were plotted against sample size, it was apparent that rarefaction predicted more species per sample than was actually found in all but those tows with the smallest catches.

Further sampling of the fauna would add new species records to the faunal list in Table 2.2, but at tremendous effort and a very slow rate. The rarefaction curve in Figure 2.1 can be used as an estimator of the amount of effort required to capture additional new records (Simberloff 1972). It indicates that an additional directed survey of 25-30 samples would capture only one or two new species. This poor rate of return is supported by the number of new records resulting from sampling efforts outside this study. Collections from three cruises sampling larval squid in the Slope Sea in 1979 (*Belogorsk* Be7902, Be7903) and 1986 (*Gadus Atlantica* G121), as well as a deep bottom survey of the slope in 1995 (*Cape Chidley* C020) were also examined by the author, though these data were not included here. These four cruises provide eight species additional to present collections: *Dolichopteryx binocularis*, *Opisthoproctus soleatus, Diaphus taaningi, Microstoma microstoma, Xenodermichthys copei, Eustomias lipochirus, Thalassobathia pelagica,* and an unidentified cetomimid. Scott and Scott (1988) list an additional nine species: *Polymetme corythaeola, Eustomias fissibarbis, Aristostomias photodactylus, Aristostomias polydactylus, Trigonolampa miriceps, Melamphaes microps, Poromitra crassiceps, Benthodesmus tenuis,* and *Cubiceps capensis;* all are records based upon one to a few specimens.

Claims for the comprehensiveness of this survey should perhaps be restricted to those species which vertically migrate into the upper 200 m as juveniles or adults. Ten of the 17 species listed above which were not caught in present surveys (*O. soleatus, Eustomias* spp. *T. pelagica,* the cetomimid, *T. miriceps, Aristostomias* spp., *M. microps,* and *P. crassiceps*) may have been missed because they tend to be bathypelagic as adults or do not necessarily migrate into the upper 200 m (Cohen 1984; Gibbs 1984c; Nielson 1986; Paxton 1986; Maul 1986). Excluding *D. taaningi, X. copei* and *P. corythaeola* as benthopelagic (Nafpaktitis et al. 1977; Badcock 1984; Markle and Quero 1984) and *D. binocularis* as fragile and rare (Cohen 1984), leaves only *M. microstoma, B. tenuis* and *C. capensis* as species expected to occur here but not sampled in this study. A few additional residents of the Slope Sea may appear with more sampling, but it is more likely that any new records of mesopelagic species will be expatriates from regions adjacent to the Slope Sea. Lack of asymptotes in the rarefaction curves for the three water masses support this conclusion;

these curves indicate that the LSW, WSW and GS are open systems exchanging species between them. Some additional species of northern and/or eastern Atlantic origin may be injected into the WSW by the Labrador Current but new records are most likely to be species of subtropical or tropical origin contributed by the Gulf Stream, which is a carrier of expatriated species (Markle et al. 1980) and was the most poorly sampled of the three water masses.

2.4.2 Variation in species composition and abundance

Depth: Differences between the two sampling strategies: shallow oblique tows at night, and deep horizontal tows during the day, are a likely cause of the observed higher night catches. Species depth ranges are narrower at night, with a greater overlap between species, than in the day (Paxton 1967; Karnella 1987; Gartner et al. 1987). Day tows sampled horizontally within a narrow vertical band, so even with the net open during haulback, it could effectively sample the depth of maximum abundance of only a few species. Night tows obliquely sampling a 200 m stratum would pass through the depths at which many mesopelagic species, particularly myctophids, are very abundant. It was suggested earlier that the high catch rates of cruise H127 were due to the relatively shallower towing depth; other studies have shown that several of the species also abundant in the Slope Water occur in high numbers between the surface and depths shallower than 50 m (Backus et al. 1977; Gartner et al. 1987;

Karnella 1987). Gartner et al. (1989) recommended that studies on myctophid distributions include neuston collections because of the several genera in which a significant proportion of the population were found at the surface at night. For example, *M. punctatum* was the second most abundant species in collections from the subpolar region of the North Atlantic (Backus et al. 1977), compared to fourth in the LSW in the present study. It was mainly taken in neuston nets (Nafpaktitis et al. 1977), and hence less abundant in collections by McKelvie (1985b) and this study which did not sample the surface.

The total number of species in shallow and deep tows was similar but the type of species differed. Myctophids dominate the shallower depths but also occupy a wide vertical range with many species occurring in the deepest tows. The mesopelagic families Gonostomatidae, Sternoptychidae, Melanostomiidae and Malacosteidae are composed of species in which populations do not vertically migrate, or partial populations migrate to above 200 m, or to intermediate depths of 300-500 m (Badcock and Merrett 1976; Howell and Krueger 1987). These families were abundant in samples from below 600 m.

Higher catch volumes in deep tows are due partially to differences in species morphology since a number of the species more common in the deeper tows, such as the eels and stomiatoids, have a larger average body size than the myctophids of the shallower tows. Childress et al. (1990) suggest that deep dwelling pelagic fish species grow to a larger maximum size than species which vertically migrate to the near surface, by incorporating water into their tissues. The latter face higher predation pressure and must use energetically more expensive fat or protein to maintain muscular systems. This raises the interesting possibility that deep dwelling species may be slower and less able to avoid an approaching trawl than the more robust vertical migrators. With respect to species common to all tow depths, increasing body size with increasing depth whereby larger individuals of a given species reside deeper and migrate into shallow depths less frequently has been demonstrated by many studies (e.g., Badcock 1970; Clarke 1973, 1974; Willis and Pearcy 1980; Goodyear et al. 1971; Karnella 1987; Gartner et al. 1987; Craddock et al. 1992) but this was not examined in the present study.

Season: Shifts in species dominance from winter through summer to autumn surveys were expected due to variation in lifespan and spawning times between species, and the lower effective size limit of the IYGPT (ca. 20 mm). Several of the abundant species captured in the February through April cruises, i.e. *B. glaciale, C. maderensis,* and *Gonostoma elongatum* have life cycles greater than one year (Halliday 1970; Clarke 1974; Lancraft et al. 1988; Linkowski et al. 1993) so at least part of the population would be available to the IYGPT all year. The species predominant in the late summer cruises were *H. hygomii* and *L. dofleini* which have one year life cycles and spawn in the fall and winter (Karnella 1987). Thus, only juveniles would be in the population during winter-spring months, and these would be too small to be caught in the trawl. *Hygophum benoiti* is an annual species which is temporally segregated from its congener, *H. hygomii*, by spawning in spring. Subadults (23-30 mm) and adults of this species are most abundant in winter months (Karnella 1987), whereas the smaller life stages, not catchable in the IYGPT are present in the summer. Two environmental factors which could affect species richness and composition are seasonal variability in the temperature structure of the WSW, and variation in the rate of transport of species into the WSW from the adjacent water masses. The relative importance of species-specific life histories, seasonal cooling of the WSW, and passive transport into WSW on faunal composition is not discernible from the broad, descriptive sampling design used here. Their effects are considered in Chapter 3, in which the vertical structure of the fauna over time is examined using a trawl capable of capturing smaller individuals than the IYGPT, and Chapter 4 which relates spatial distributions of species to the positions of the hydrographic fronts.

2.4.3 Comparisons with previous studies

Labrador Slope Water: Previous faunal studies also describe *B. glaciale* as the most abundant species in the LSW, contributing 74-83% of the total catch (Table 2.12). Higher species richness reported in this study is due probably to the greater sampling effort (58 tows vs. 4 to 16 previously).

Backus et al. (1977) include the LSW in the Atlantic Subarctic, which they characterise as a region of low faunal diversity dominated by *B. glaciale.* The Newfoundland Basin, a more northerly portion of the subarctic region which supplies the LSW with water and accompanying fauna, also has a depauperate fauna dominated by *B. glaciale* (McKelvie 1985b). Average species richness of the Newfoundland Basin (14.2 species/tow) was similar to the LSW (14.9 species/tow). Relative abundance was less even in the Newfoundland Basin where *B. glaciale* contributed 83% of the total catch (McKelvie 1985b), compared to 74% in the LSW off the Scotian Shelf, a difference probably due to the broader seasonal coverage by this study.

Warm Slope Water: The most abundant species found in WSW in this study, *C. maderensis, B. glaciale* and *L. dofleini,* are similar to those previously reported for this water mass, with differences in ranking attributable to tow depth and season of sampling (Table 2.12). *Benthosema glaciale* and *Cyclothone* spp. dominated the catch in surveys using oblique or horizontal tows predominantly at depths greater than 200 m. *Lobianchia dofleini* was the most abundant species in two surveys, one of which occurred during the summer and fall (Jahn and Backus 1976; the other by Backus et al. 1970 does not supply station data).

Table 2 12 Comparison of species richness (no spec) and species ranking from this study with published results of other mesopelagic surveys of the Slope Sea, summarized by sampling location (LSW=Labrador Slope Water, WSW=Warm Slope Water, GS=Gulf Stream and warm core rings). Tow type (depth in metres) h=horizontal, o=oblique, n=number of samples, percent contribution to total catch, if available, follows species name

Location	Tow type	n	No spec	First Rank	Second Rank	Third Rank	Fourth Rank	Fifth Rank	Author
LSW	0 200 h	4	56	*B glaciale* 82	*C maderensis* 13	*S boa* 1	*L crocodilus* 1	*L. pusillus* 1	Backus et al 1970
	500-1000 h	10	51	*B glaciale* 83	*S boa* 4	*B euryops* 3	*P arcticum* 3	*C sloani* 2	McKelvie 1985b
	100-1000 h	16	28	*B glaciale*	*P arcticum*	*B euryops*	*S beanii*	*S boa*	McKelvie 1985a
	0-300 o	58	102	*B glaciale* 74	*C maderensis* 8	*N rissoi* 4	*M punctatum* 3	*L dofleini* 2	This study
WSW	0-1000 o	13	87	*Cyclothone*	*B glaciale*	*C maderensis*	*S diaphana*	*L. dofleini*	Jahn 1976
	0 1000 h	24	121	*L dofleini*	*B glaciale*	*C maderensis*	*N resplendens*	*G elongatum*	Jahn and Backus 1976
	0-1000 o	12	80	*B glaciale* 51	*C maderensis* 13	*H hygomii* 7	*L dofleini* 6	*L. alatus* 3	Backus and Craddock 1982
	0-200 h	5	87	*L dofleini* 27	*C maderensis* 20	*L pusillus* 6	*G elongatum* 5	*B glaciale* 5	Backus et al 1970
	500 h	17	80	*B glaciale* 61	*Cyclothone* 10	*C maderensis* 3	*C sloani* 2	*H benoiti* 2	McKelvie 1985b
	0-1000 o	1	NA	*Cyclothone* 65	*C maderensis* 12	*B glaciale* 6	*H benoiti* 1	*S diaphana* 1	Craddock et al 1992
	0-300 o	149	214	*C maderensis* 39	*L dofleini* 18	*B glaciale* 13	*H hygomii* 6	*N resplendens* 4	This study
GS	0-1000 h	7	104	*D atlanticus*	*C warmingii*	*L. guentheri*	*C maderensis*	*G elongatum*	Jahn and Backus 1976
	100-1000 h	18	50	*C maderensis*	*C warmingii*	*H benoiti*	*H hygomii*	*L guentheri*	McKelvie 1985a
	0 300 o	10	123	*H hygomii* 10	*L dofleini* 10	*C warmingii* 9	*D mollis* 9	*B indicus* 8	This study

Gulf Stream and Warm Core Rings: The GS/WCR fauna cannot be characterised from this study since the GS was poorly sampled in terms of the number of samples and their location. Sampling was at the northern margin of the GS or within WCRs, where species composition would be modified either by the proximity of the WSW, or the ring core of Sargasso Sea origin. Rings are regions of mixing between faunas of the WSW and those expatriated from the Sargasso and Caribbean Seas, so the observed species composition is a feature of the ring's age and the sampling position within the ring (Olson and Backus 1985; Backus 1987). Although more species were collected in the WSW, the numbers of species per tow and the expected number of species were significantly higher in GS samples, indicating that increased sampling would have resulted in a species richness surpassing that of the WSW.

Only two of the five ranking species found in GS in this study, *C. warmingii* and *H. hygomii,* were similarly ranked in other surveys of the GS fauna (Table 2.12). The top ranking species reported by Jahn and Backus (1976), *D. atlanticus,* is a small species. It may have been more abundant in their survey because their trawl was equipped with a finer mesh net than the IYGPT used here. In general, the relative abundance of the GS and WCR fauna must be seasonally variable due to the contribution of fauna from the Sargasso Sea. None of the three surveys of the GS (Table 2.12) definitively describes its fauna since they are based upon 7-18 samples taken in several different months. Jahn and Backus (1976) found the GS fauna was not just a mixture of the Slope Water and Sargasso Sea faunas, presumably because it carries the remains of a tropical fauna (Backus 1987).

In conclusion, the ten surveys were sufficient to characterize the fauna of the Slope Sea, providing a close to comprehensive list. Additional sampling will discover new species records infrequently of one or a few specimens (probably expatriated species of subtropical or tropical origin), however, there are no commonly occurring species which have not yet been recorded. Choices made in sampling strategy affected the perceived faunal composition and relative abundance. The present study was most effective in identifying those elements of the fish fauna of the WSW which attain lengths greater than 2 cm, and vertically migrate into the upper few hundred metres at night.

Chapter 3: Vertical distribution of the mesopelagic fauna of the Slope Sea off Atlantic Canada

3.1 Introduction

Studies on the vertical distributions of mesopelagic fish have shown that depth ranges are species-specific. Many, but not all species undergo diurnal migrations during which all or part of the population migrates to shallower depths at night than those occupied during the day. Variations in preferred day and night depths within species have been correlated with physical and biological factors such as season, ontogeny, water temperature, productivity and latitude. Knowledge of vertical distribution patterns is therefore an important part of understanding faunal composition and relative abundance. Any study based solely on samples taken horizontally at a few depths will give an incomplete view. Some of the faunal characteristics described in Chapter 2 were uncertain, due to the sampling strategy and trawl employed. As most samples were taken from shallow depths at night, non-migrating species which inhabited greater depths, such as *Cyclothone,* were under-represented. Capture efficiency of the trawl decreased with small individuals, so the relative abundance of species which are predominantly less than 2 cm in maximum length (e.g. the myctophids *Notolychnus valdiviae, Diogenichthys atlanticus*) were almost certainly underestimated. Observed seasonal variations in relative abundance are likely overemphasized by this bias toward larger animals and therefore older, mature life stages.

The few vertical distribution studies of the mesopelagic fauna off the Scotian Shelf were concerned mainly with the myctophid *Benthosema glaciale* (Halliday 1970; Sameoto 1982, 1988). However, there is information for several of the species captured in the present study from the Slope Water, the Sargasso Sea, Mediterranean Sea and the Northeast Atlantic, (Badcock 1970; Goodyear et al. 1972; Badcock and Merrett 1976, 1977; Nafpaktitis et al. 1977; Roe and Badcock 1984; Karnella 1987; Craddock et al. 1992).

This chapter characterises the mesopelagic ichthyofauna captured using a Tucker trawl (Davies and Barham 1969), a small midwater trawl equipped with a fine mesh net and an mouth opening-closing device, during the standard surveys conducted in 1988-89. Vertical distribution and variation in mesopelagic fish species composition, abundance and size range with depth are described for three surveys on which sampling was adequate for these purposes. Samples taken by the Tucker trawl are compared to IYGPT samples taken at similar locations.

3.2 Methods

Mesopelagic fish species were collected in 112 Tucker trawl hauls during the six standard surveys (Table 3.1). At one or more stations during each cruise, the trawl, equipped with an mouth opening-closing device, was towed repeatedly in horizontal tows at discrete depths between 50 and 600 m.

Table 3.1. Distribution of 112 Tucker Trawl samples by tow depth (m) and diel period collected on the six surveys between February 1988 and August 1989. Numbers indicate numbers of samples at that depth. D - daytime; N - nighttime.

Cruise	N096		N110		N112		N119		N122		N126			
Date	Feb.		Oct.		Dec.		Apr.		Jun.		Aug.		Total	
Depth (m)	D	N	D	N	D	N	D	N	D	N	D	N	D	N
50		5		1			2	2	2	2	2	2	6	12
100	1	4					2	2	2	2	2	2	7	10
150	1	1		1	1	1		2					2	5
200	2	2		1			2	2	2	1	2	2	8	8
250						1							0	1
300	3		1		1		2	1	2	2	2	2	11	5
350							2						2	0
400				1	1	2	2	1					3	4
450	2				1				1	1	3	1	7	2
500	2				1		2		1		1		7	0
600	1						3		2	2	2	2	8	4
Total	12	12	1	4	5	4	17	10	12	10	14	11	61	51

Three fixed stations were fished for 24 hours on the first cruise in February (N096), two near the 1000 m depth contour in Labrador-Slope water (LSW) and one near the Gulf Stream in warm Slope water (WSW). One station in each water mass was fished in the second cruise (October, N110), and a single WSW station in the four subsequent cruises (Fig. 3.1). Total time spent at a station was increased to approximately 48 hours during the last three surveys (N119, N122 and N126), and tows at each depth were repeated. No tows were made within the hour before or following sunrise or sunset. Temperature and salinity data were collected to 1000 m at dawn and dusk using a Conductivity-Temperature-Depth (CTD) probe.

The mouth of the Tucker trawl was 2.5 m wide by 2 m high. The net used in all surveys was 5 m long with a mesh size of 1.6 mm (bar) except that that used on cruise N110 had a mesh size of 12.75 mm (bar). A mechanical timing device mounted ahead of the trawl released the horizontal bars which opened and closed the mouth of the net at depth. All tows were of 30 minutes duration.

Net depth was monitored on most tows by SCANMAR (nine tows by a hardwire midwater trawl headline transducer) with a time-depth recorder (TDR) as a backup. Tow depth was controlled by varying the amount of warp released while keeping the ship's speed constant. Warp length, ship speed and tow depth were averaged for each tow from observations every minute. Average ship speed ranged from 1.8 to 4.3 knots between tows, and the grand

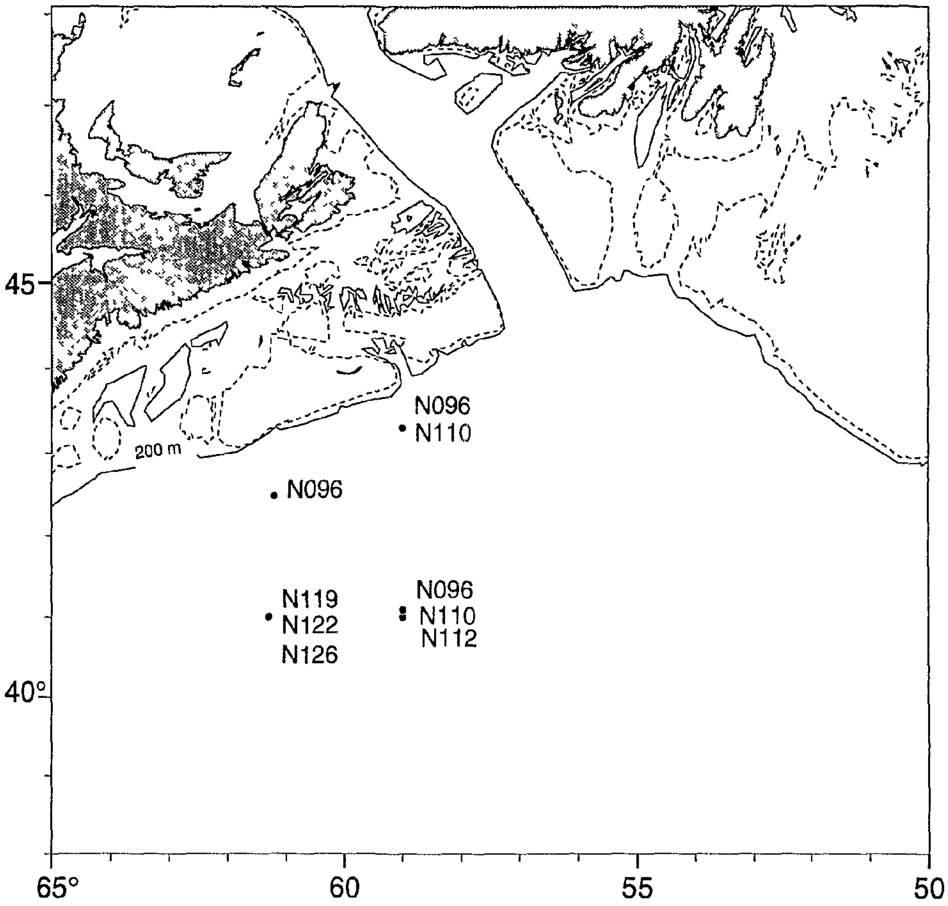


Figure 3.1. Locations sampled in the Slope Sea off Atlantic Canada by Tucker trawl between February 1988 and August 1989.

mean and its standard deviation for all tows was 2.77 ± 0.44 knots. The largest deviations from average depth observed were 30 m for tows at depths less than 300 m and 50 m for deeper tows, but the depth deviation was smaller for most tows. Tows were only included in this analysis if their average depth was within 10 metres of the assigned depth. Three tows on which depth-monitoring devices failed were assigned depths using a warp-length relationship generated from 48 monitored tows. Ship's heading was varied to maintain control over towing speed but all tows bisected the station's coordinates.

Volumes and numbers of individuals captured are reported on a per 30 minute tow basis because the amount of water filtered during each individual tow could not be measured. A TSK flowmeter mounted on the towing cable just ahead of the trawl and triggered by wires attached to the free falling bars, was so unreliable that it was removed after the first two cruises. Observations of a telemetered Tucker trawl towed at 10 metres depth indicated that the angle of the net's mouth from vertical when fishing was positively related to towing speed (J. McRuer, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication). The effective fishing area was 3.5 m^2 at 2.7 knots, decreasing to 2.8 m^2 at speeds over 4.0 knots. However, the vertical movement of the trawl and the angle of the trawl is probably less affected by towing speed than by the amount of towed cable as towing depth is increased. The Tucker trawl used in this study would not descend below 600 m. It was probably almost vertical at this depth (J. McRuer, personal communication), and therefore filtering more water than would be estimated from the towing speed.

The IYGPT was deployed at some of the same depths and sampling locations as the Tucker trawl during the June and August 1989 surveys. In June, these were single horizontal tows for 30 minutes at 100 and 200 m (night), and 300, 450 and 600 m (day). A single three-step oblique tow, with ten minute steps at 200, 100, 50 m depths was conducted in June and August.

A measure of relative volume of water filtered was required to compare catch size at a given depth between the Tucker trawl and IYGPT. The area sampled by the IYGPT may be larger than its mouth area because its warps, doors and bridles are ahead of the mouth and can herd fish into the net (Kenchington 1989). In contrast, the bridle of the Tucker trawl is above the mouth so it contributes relatively little to the magnitude of the area sampled (Kashkin and Parin 1983). However, in the absence of data on possible herding effects, comparisons were based on mouth area only. Assuming 100% filtering efficiency, and a mouth area of 3.5 m^2 at the average towing speed of 2.77 knots, the Tucker trawl sampled about 9×10^3 m^3 in a 30 minute tow. At 2.5 knots, the IYGPT sampled 228×10^3 m^3 (based on a mouth area of 98 m^2; Chapter 2). Thus the volume of water filtered by the IYGPT was taken as 25 times that of the Tucker trawl. The performance of the two trawls was compared by dividing the IYGPT catch rate by this factor (adjusted catch rate).

The catch was processed as described in Chapter 2. Displacement volumes of the total mesopelagic fish component were measured (+/- 1 ml) for the samples from all Tucker trawl tows except those from February (N096) and December (N110), after non-mesopelagic species were removed (listed in Appendix 1). Minimum and maximum standard lengths to the nearest millimetre were measured for each species lot; head or total length for eels, standard length for all other species. Two life stages were assigned to the few species exhibiting strong dimorphism: larvae - premetamorphic individuals which had not yet developed the full complement of photophores or adult coloration (all of these were postlarvae which had resorbed the yolksac) and juvenile/adult - postmetamorphic individuals with fully developed photophores and pigment patterns.

Average catch (numbers fish per tow) and average volume (ml per tow) at depth were calculated by combining samples for the same nominal depth and diel phase when more than one sample was available. This applied to the three surveys in April (N119), June (N122) and August (N126) as only then were sufficient samples collected to describe and compare day versus night distributions. The relative abundance of a species was determined by its contribution in numbers to total catch within a depth stratum and diel sampling phase. A few studies have related shifts in vertical distributions of some mesopelagic species to the lunar phase (Badcock 1970; Clarke 1973; Linkowski et al. 1993). Too few samples were taken to consider lunar effects on vertical distributions here since both the April and August surveys occurred during full moon, and the June survey occurred during the first quarter.

Oceanography at 41°00′ N 61°30′ W during April, June and August surveys

Variation in temperature and salinity in the upper 200 m of the water column was observed during the April and June surveys, but not in August. In April, temperatures in the top 50 m increased from 13 to 15 °C during the sampling period, and the volume of high salinity water (> 35.5) in the upper 200 m also increased (Fig. 3.2a). In June, a layer of cool, low salinity water (11°C, <34.5) occurred at 50 m about midway through the sampling period. Salinity was about 35.0 throughout the water column on the third and final day of sampling (Fig 3.2b). In August, there was little change in temperature and salinity over the sampling period (Fig. 3.2c).

Variation in temperatures and salinities between the surveys was slight. Surface temperatures rose from 14-15 °C in April, to 23 °C in August. A thermocline developed by June at 20-50 m, and had intensified by August. Temperatures at depths below 200 m were almost identical in June and August, and about a degree warmer than in April. In all sampling periods, water characteristics were indicative of Warm Slope Water (Halliday et al. 1995).

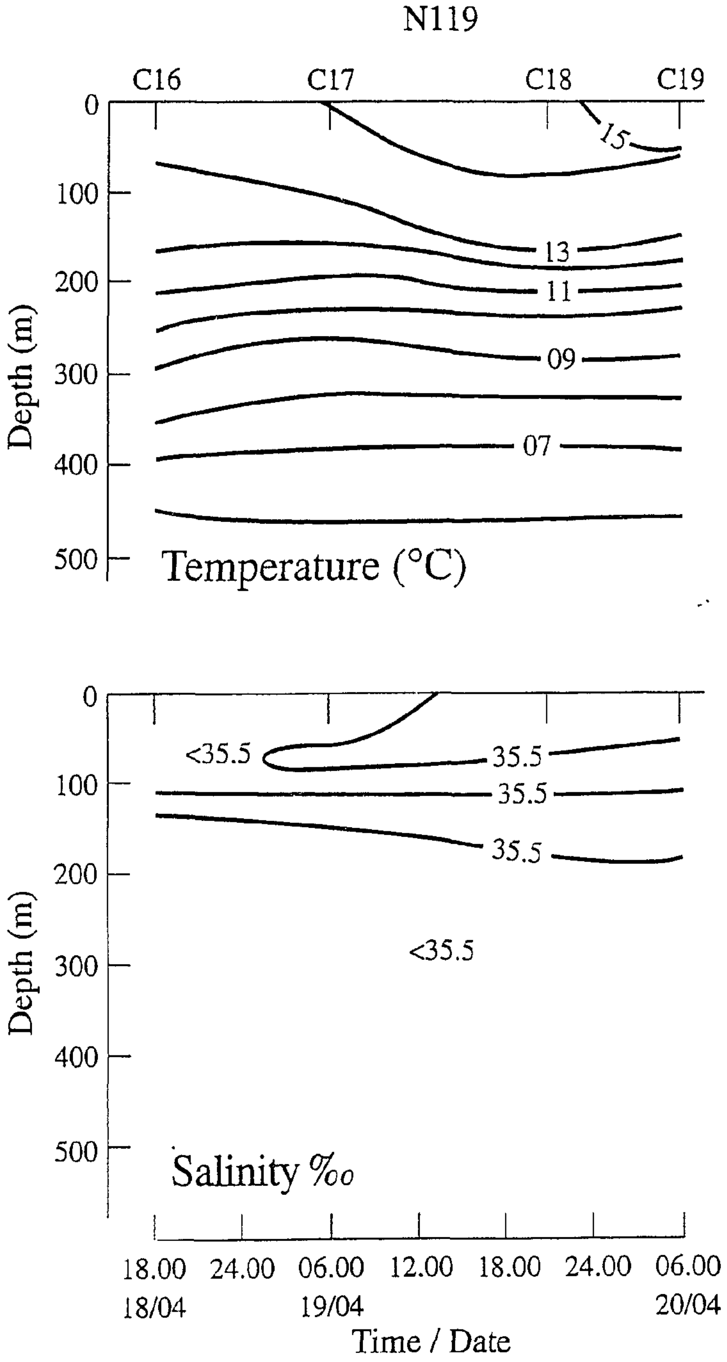


Figure 3.2. Temporal variation in temperature and salinity at 41°00'N 61°30'W (from Halliday et al. 1995) in April, June and August 1989. a). 18-20 April 1989 (cruise N119).

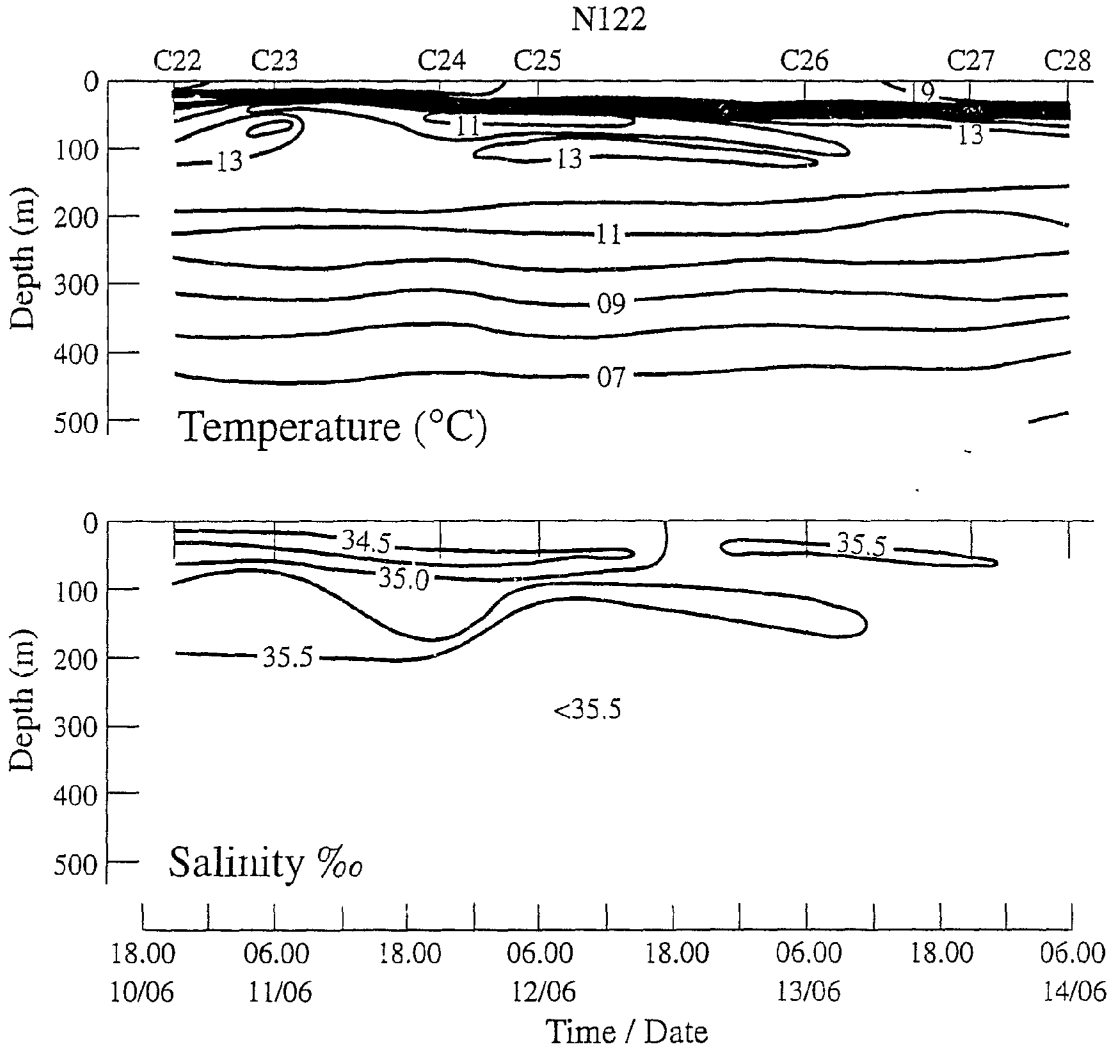


Figure 3.2 cont. b) 10-14 June 1989 (cruise N122).

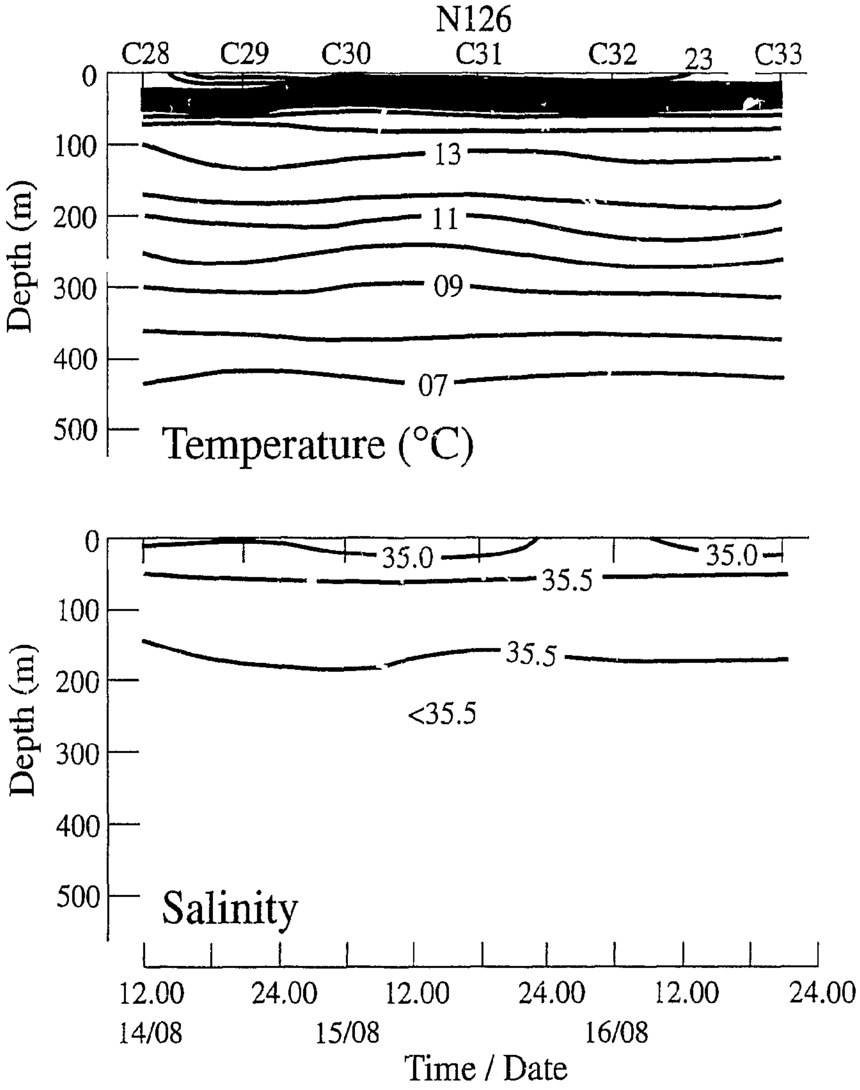


Figure 3.2 cont. c) 14-16 August 1989 (cruise N126).

3.3 Results

3.3.1 Faunal composition

Species composition of the midwater fish fauna, as portrayed by Tucker trawl samples, is based upon the 113 samples from all six surveys. A total of 14,349 individuals were captured on these surveys, representing 93 species and 22 families (Table 3.2). The three most abundant species were *Benthosema glaciale, Cyclothone* spp. and *Ceratoscopelus maderensis,* in decreasing order of abundance. These species collectively comprised 86 % of the total catch. An order of magnitude difference occurred between the numbers of *C. maderensis* captured and the next highest ranked species. The next most abundant species were *Notolepis rissoi* (2.5% of total catch), *Lobianchia dofleini* (2.0%) and *Diogenichthys atlanticus* (1.6%). *Benthosema glaciale* and *C. maderensis* were the most frequently occurring species, appearing in 58% and 55% of the samples, respectively. Forty-one species (44% of all species captured) occurred only once or twice in the samples (Table 3.2).

3.3.2 Vertical distribution of numbers and volume in April, June and August

In April, sampling coverage of the water column was more thorough in the day than at night. Seventeen day tows sampled depths between 50 and 600 m, compared to ten tows at depths of 50 to 400 m at night (Table 3.1). In June and August, effort was similarly distributed with respect to diurnal

Table 3.2. Total numbers and percent frequency of occurrence (%FO) of mesopelagic fish fauna in 112 Tucker Trawl collections in the Slope Sea between February 1988 and August 1989. Twenty most abundant species are ranked.

Family Species	Total	Rank	%Occur.
Nemichythidae			
Nemichthys scolopaceus	6		5.4
Derichthyidae			
Derichthys serpentinus	2		1.8
Nessorhamphus ingolfianus	3		2.7
Serrivomeridae			
Serrivomer beari	9		8.0
Bathylagidae			
Bathylagus compsus	2		1.8
Gonostomatidae			
Cyclothone spp.	3858	2	30.4
Diplophos taenia	1		0.9
Gonostoma atlanticum	3		1.8
Gonostoma elongatum	68	10	24.1
Margrethia obtusirostra	1		0.9
Sternoptychidae			
Argyropelecus aculeatus	27	18	15.2
Argyropelecus hemigymnus	41	14.5	16.1
Maurolicus muelleri	9		4.5
Polyipnus asteroides	41	14.5	7.1
Sternoptyx diaphana	23		9.8
Valenciennellus tripunctulatus	21	20	9.8
Photichthyidae			
Ichthyococcus ovatus	1		0.9
Pollichthys mauli	6		4.5
Vinciguerria attenuata	15		6.3
Vinciguerria nimbaria	9		4.5
Vinciguerria poweriae	56	11	8.0
Chauliodontidae			
Chauliodus sloani	38	16	21.4
Stomiidae			
Stomias boa ferox	34	17	17.9
Melanostomiidae			
Bathophilus metallicus	1		0.9
Chirostomias pliopterus	1		0.9
Melanostomias spilorhynchus	4		2.7
Melanostomias valdiviae	1		0.9
Photonectes margarita	1		0.9

Table 2.3 cont

Family Species	Total	Rank	%Occur
Melanostomiidae cont			
Thysanactis dentex	1		0.9
Malacosteidae			
Aristostomias lunifer	1		0.9
Aristostomias tittmanni	1		0.9
Malacosteus niger	2		1.8
Photostomias guernei	3		1.8
Scoplarchidae			
Scopelarchus analis	2		0.9
Notosudidae			
Ahliesaurus berryi	1		0.9
Scopelosaurus lepidus	1		0.9
Paralepididae			
Lestidiops affinis	5		3.6
Macroparalepis affine	4		3.6
Notolepis rissoi	359	4	33.9
Paralepis coregonoides	13		3.6
Sudis hyalina	7		2.7
Evermanellidae			
Evermanella balboa	1		0.9
Evermanella indica	1		0.9
Omosudidae			
Omosudis lowei	1		0.9
Myctophidae			
Benthosema glaciale	4881	1	58.0
Benthosema suborbitale	24	19	8.0
Bolinichthys indicus	18		6.3
Bolinichthys supralateralis	10		6.3
Centrobranchus nigro-ocellatus	1		0.9
Ceratoscopelus maderensis	3481	3	55.4
Ceratoscopelus warmingii	18		6.3
Diaphus dumerilii	14		6.3
Diaphus effulgens	9		7.1
Diaphus metopoclampus	4		2.7
Diaphus mollis	5		2.7
Diaphus rafinesquii	116	7	12.5
Diaphus splendidus	2		1.8
Diogenichthys atlanticus	227	6	18.8
Gonichthys coccoi	2		1.8
Hygophum benoiti	9		6.3

Table 3.2 cont.

Family Species	Total	Rank	%Occur.
Myctophidae cont.			
Hygophum hygomii	71	9	17.0
Hygophum reinhardtii	1		0.9
Hygophum taaningi	3		2.7
Lampadena speculigera	1		0.9
Lampanyctus alatus	20		11.6
Lampanyctus ater	6		3.6
Lampanyctus crocodilus	36	15	7.1
Lampanyctus photonotus	3		2.7
Lampanyctus pusillus	50	12.5	12.5
Lepidophanes guentheri	50	12.5	9.8
Lobianchia dofleini	296	5	19.6
Lobianchia gemellerii	8		5.4
Loweina rara	7		6.3
Myctophum affine	1		0.9
Myctophum obtusirostre	1		0.9
Myctophum punctatum	2		0.9
Notolychnus valdiviae	81	8	12.5
Notoscopelus caudispinosus	2		1.8
Notoscopelus elongatus kroyeri	2		0.9
Notoscopelus resplendens	11		4.5
Symbolophorus veranyi	1		0.9
Taaningichthys minimus	4		2.7
Melamphaidae			
Melamphaes typhlops	1		0.9
Poromitra capito	1		0.9
Scopeloberyx opisthopterus	1		0.9
Scopelogadus beanii	1		0.9
Scopelogadus mizolepis	1		0.9
Percichthyidae			
Howella sherborni	12		7.1
Gempylidae			
Diplospinus multistriatus	11		4.5
Gempylus serpens	1		0.9
Nealotus tripes	1		0.9
Nomeidae			
Psenes pellucidus	2		0.9
Ariommatidae			
Ariomma sp.	1		0.9

period and depth as approximately equal numbers of day and night tows sampled depths between 50 and 600 m (Table 3.1).

In April at night, highest catch rate occurred at 50 m (60 fish/tow). Catch rates declined to half that level at 150 m, and were very low at 200 and 300 m (Fig. 3.3). A catch of 30 fish in the single 400 m tow was similar to the averaged catch at 150 m. Sample volume was also highest at night at 50 m, and decreased at greater depths (Fig. 3.4). The most abundant species with depth were *B. glaciale* at 50 m (20 % of total catch), *N. rissoi* at 100 m (37%) and 150 m (66%), and *Cyclothone spp.* (97%) at 400 m.

Catches in April day tows at depths above 350 m were very low, increased to a high of 330 fish/tow at 500 m, and then declined about 20% at 600 m (Fig 3.3). Fish volume increased steadily with depth from 26 ml/tow at 350 m to 94 ml/tow at 600 m (Fig 3.4). *Cyclothone* spp. was the most abundant species in day samples at depths of 350 m or more, comprising 54-93% of the total catch. Increase in fish volume but not numbers between 500 and 600 m was due to the capture of 5 *Gonostoma elongatum* (123-173 mm) at 600 m compared to one (43 mm) at 500 m.

In June at night, catch rate was highest at 50 m (524 fish/tow). Catch rate decreased about 75% in the single tow at 100 m (the other 100 m tow was discarded because it collected only three fish, possibly due to the unusually high towing speed of 4.3 knots). Tows at 200 and 300 m caught very few fish (Fig 3.3). Numbers per tow increased at 450 m to 33 fish, and again at 600 m

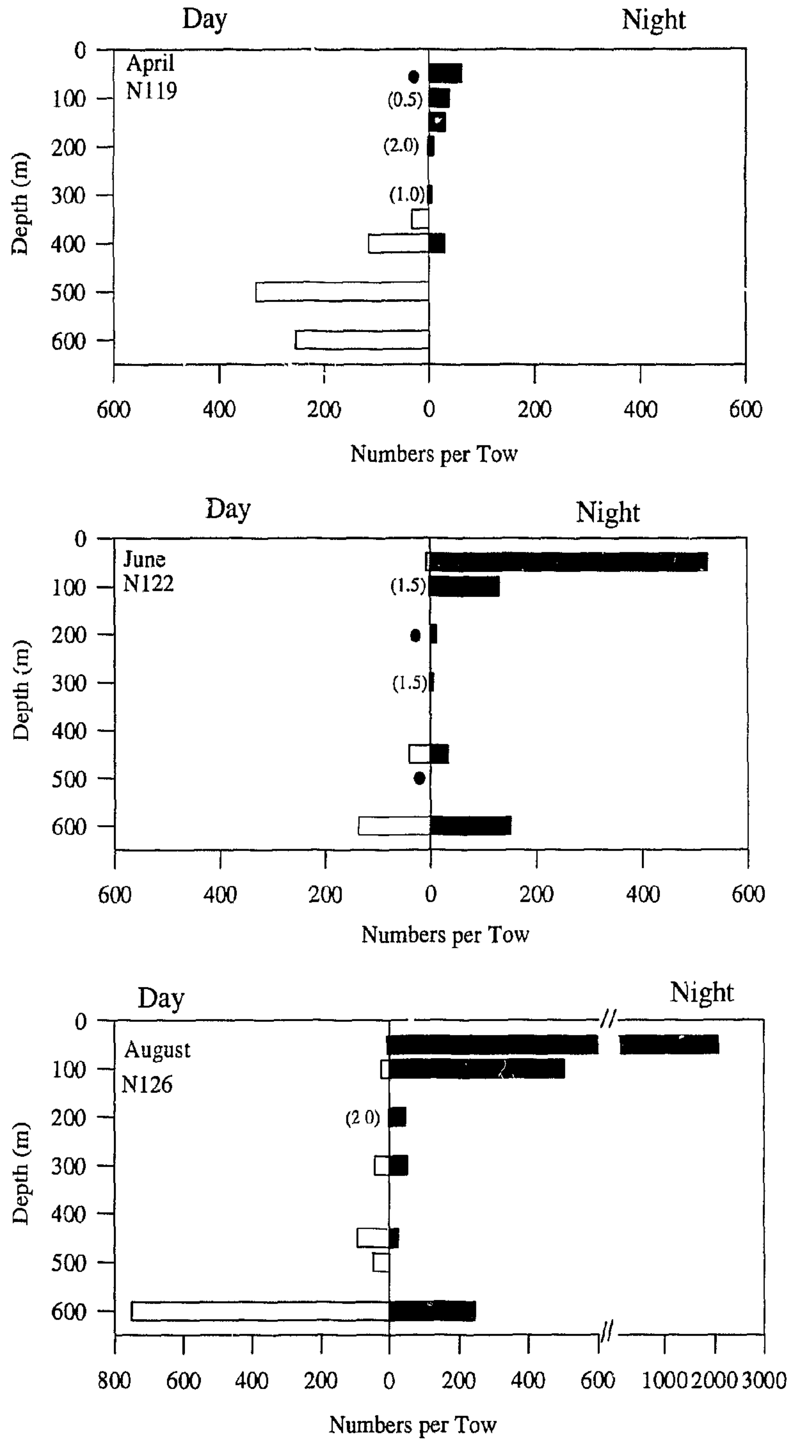


Figure 3.3. Distribution of Tucker trawl catches by depth as numbers per tow in April, June and August. Clear and solid bars represent day and night samples, respectively. ● - no catch, ( ) - low no. per tow.

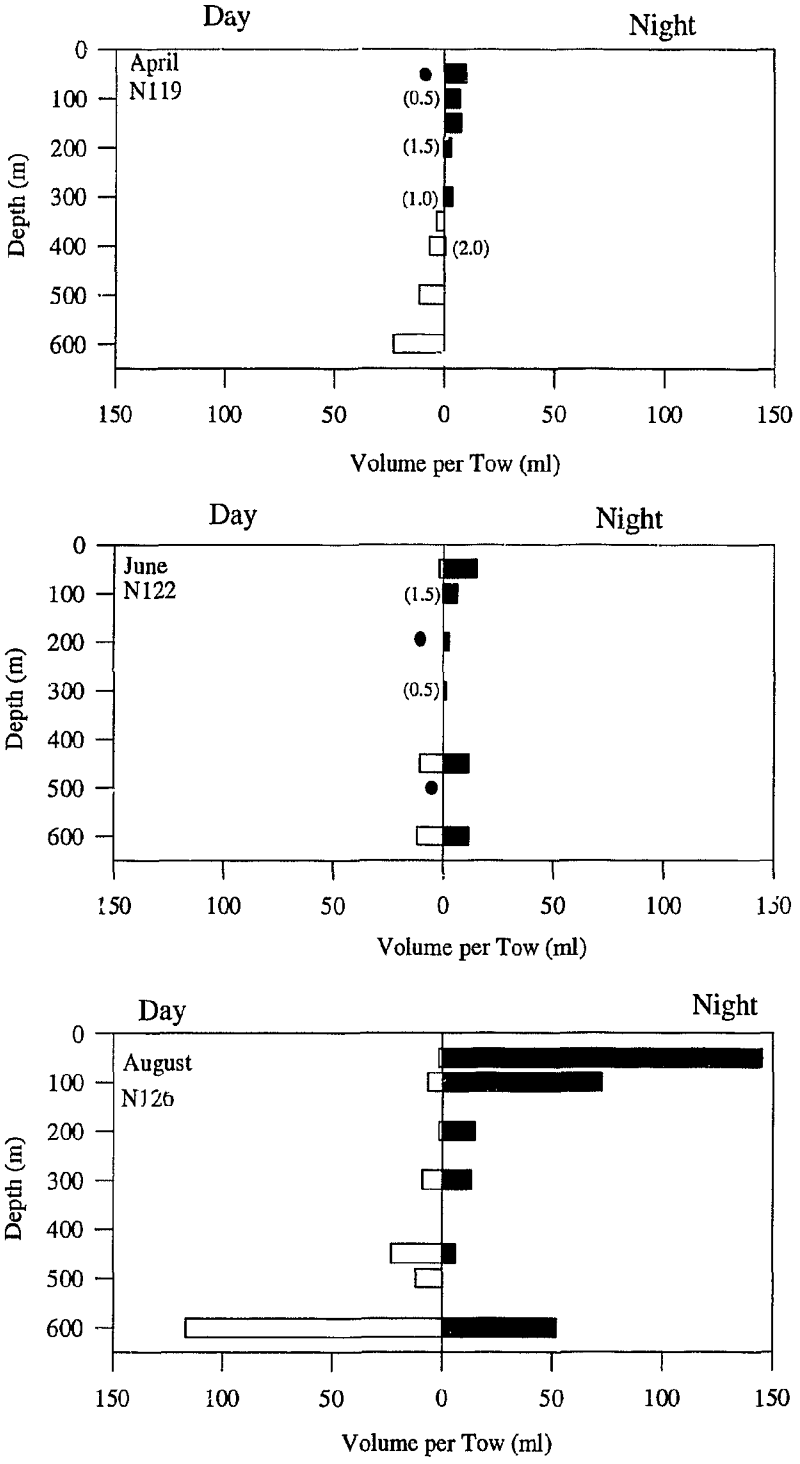


Figure 3.4. Distribution of Tucker trawl catches by depth as volume (ml) per tow in April, June and August. Clear and solid bars represent day and night samples, respectively. ● -no catch, ( ) - low vol per tow.

to 151 fish, about the same rate as observed at 100 m. Fish volume followed a similar pattern to numbers, decreasing from a high at 50 m (60 ml/tow) to negligible amounts at 300 m (Fig. 3.4). However, volume of samples from 450 and 600 m depths were similar to that at 50 m (45-60 ml/tow). The most abundant species were C. *maderensis* at 50 m (50%), *B. glaciale* at 100 m (86%), and *Cyclothone* spp. at 450 m (49%) and 600 m (88%). Equivalent fish volumes at 450 and 600 m were due to the occurrence of *B. glaciale* and *Cyclothone* spp., respectively.

In June day tows, numbers of fish captured at depths above 450 m were insignificant (Fig. 3.3). Catch rate increased from 450 to 600 m. At both depths, number of fish/tow were similar to night samples from the same depths. Fish volumes at depths above 450 m were also negligible (Fig. 3.4). At 450 and 600 m depths they were similar to night tows at the same depths (42-50 ml). The most abundant species were *Hygophum hygomii* at 450 m (43%) and *Cyclothone* spp. at 600 m (92%).

In August night tows, highest catch rates occurred at 50 m (2073 fish/tow) and declined 75% at 100 m (Fig 3.3). Catches were relatively low at depths of 200 to 450 m (26-52 fish/tow) but increased again at 600 m to about 10% of the catch at 50 m. Tow volume followed a similar pattern of rapid decrease with depth to 450 m and then increase at 600 m to about a third of the volume at 50 m (Fig. 3.3). Most abundant species at depth were *B. glaciale* at 50 m (83%) and C. *maderensis* at all other depths (56-84%) except at 450 m where *Cyclothone* spp. predominated (54%).

In August day tows, catches above 300 m were negligible. Catch rate increased from 300 m to the highest observed rates of 751 fish/tow at 600 m. Tow volume showed similar trends with the highest volumes occurring at 600 m. The most abundant species were *B. glaciale* at 300 m (46%), *Cyclothone* spp. at 450 m (54%) and *C. maderensis* at 600 m (75%, Figs. 3.3, 3.4).

Distribution patterns in numbers and volume of fish with depth were similar among the surveys. Night time distribution was bimodal as most fish were captured at 50-100 m or at 500-600 m. In the day, the highest concentrations occurred at depths of 450-600 m. Numbers and volume of fish at shallow depths at night increased greatly between April and August. In day samples, the numbers and volume of fish per tow decreased between April and June, but the highest catches occurred in August.

3.3.3 Species vertical distributions

Few species were captured with sufficient frequency to enable analysis of vertical distributions. Species discussed are restricted to the five most abundant species in Tucker trawl samples (*B. glaciale, Cyclothone* spp., *C. maderensis, N. rissoi, L. dofleini*) and a species which was very abundant in the IYGPT tows which sampled the same locations as the Tucker trawl (*H. hygomii*).

Benthosema glaciale

In April, *B. glaciale* occurred in all night tows from 300 m and shallower (although only one tow was made deeper than this, at 400 m), and all day tows deeper than 300 m (Fig. 3.5). The largest day catches were at 500 m and were approximately similar in number caught to the largest night catches, which occurred at 50 and 100 m. *Benthosema glaciale* captured were between 19 and 63 mm (the size range of specimens caught at each depth is indicated in Fig. 3.5). In night tows, individuals captured from 150-300 m were similar in size, being >43 mm, and did not include the smaller specimens (< 43 mm) seen in shallower tows. There was no obvious difference in size by depth in day catches and, in total, size ranges caught by day and night were similar.

In June, night catches in the upper 100 m increased to more than 100 fish per tow. Most of these were less than one year old, based upon their length range of 11-32 mm (Halliday 1970). A few individuals >32 mm (one year or older) were present at 300 m and deeper in day and night samples (Fig. 3.5). Few fish were captured at any depth in day samples.

Numbers of *B. glaciale* in August night tows at 50 m were about 10 times higher than in June (Fig. 3.5). Catches at 100 m at night were only about 5% of 50 m catches. The few specimens taken at 50 m in the day were newly metamorphosed juveniles, but larger fish were taken in day and night tows at greater depths.

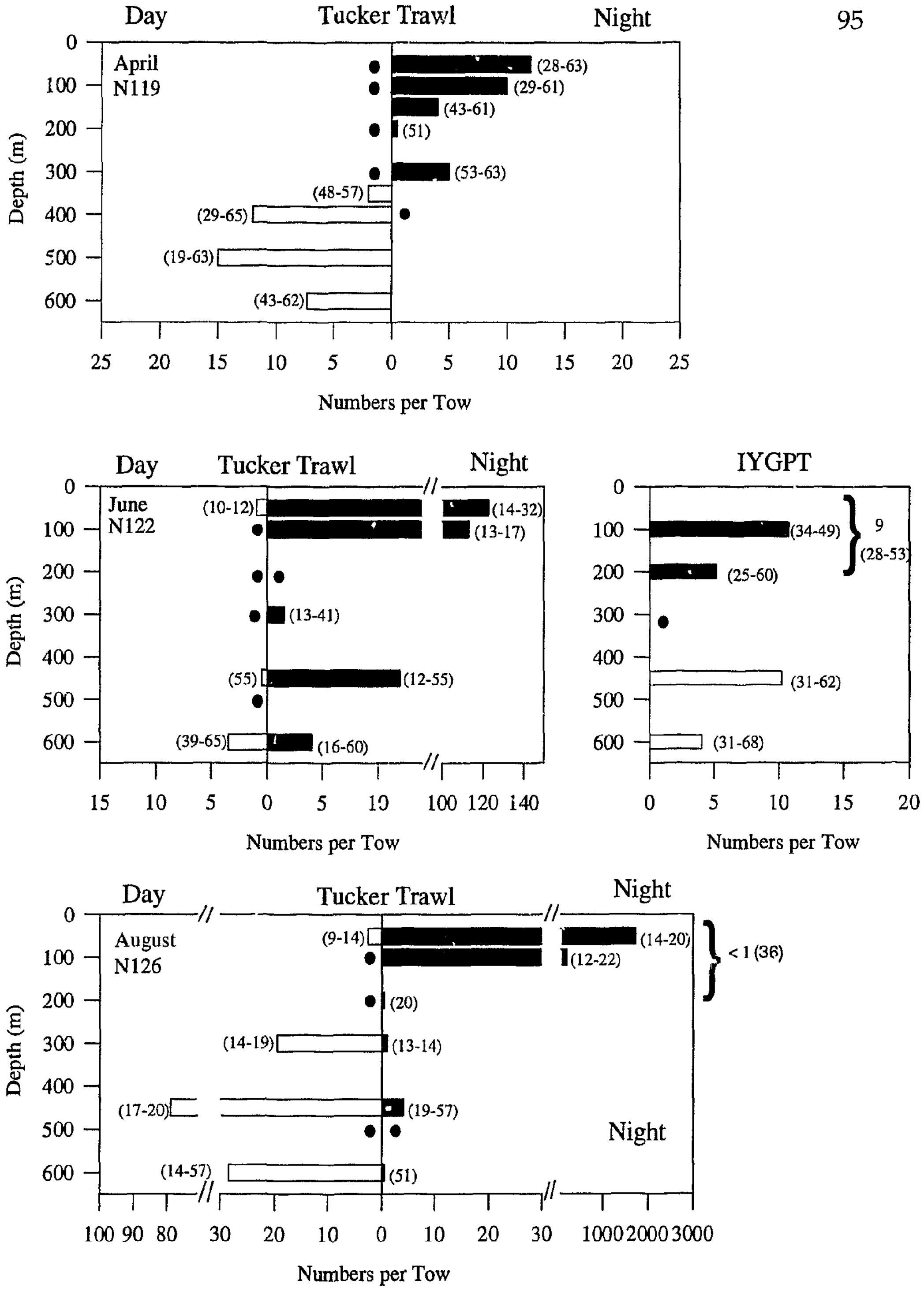


Figure 3.5. Day and night vertical distributions of *Benthosema glaciale* (mean no./tow) in April, June and August Tucker Trawl tows and adjusted catch rates in June IYGPT tows. Length range (mm) shown in brackets. Inclusive brackets show stepped oblique IYGPT catch rates in June and August. ● -none caught.

Comparison of night tows by Tucker and IYGPT nets in June at 100 m and 200 m indicates that the two nets were sampling different size groups with little overlap. The absence of large (>32 mm) *B. glaciale* in shallow night time Tucker trawl samples (when 5-10 fish could have been expected based upon adjusted IYGPT catch rates), might indicate that fish in this size range were avoiding the small trawl, except that they were captured at shallow depths in April, and at greater depths in all surveys. In the large-scale IYGPT survey during this same month the average number of *B. glaciale* also decreased, to about 15% of the number captured in April (Chapter 2, Table 2.10). Therefore, it is likely that the low catch rate in the Tucker trawl in June reflects decreasing numbers of animals older than a year occurring at shallow depths at night, rather than increased avoidance. Also in June, between 4 and 10 fish > 25 mm in length could have expected in Tucker samples from 450 and 600 m depths during day tows, based upon the adjusted catch rates in IYGPT tows at the same depths (Fig. 3.5). This expectation was met at 600 m, but at 450 m the catch was several times larger by the IYGPT than by the Tucker trawl. Both nets caught similar-sized fish at the two depths, suggesting that *B. glaciale* more effectively avoids the Tucker trawl at 450 m than at 600 m. The numbers of tows are too small to put great weight on comparisons at specific depths, but overall, it appears that the difference in catchability between gears for the larger animals is greater than that calculated on the basis of mouth area alone.

In August, the capture of a single individual in the concurrent three-step

IYGPT tow (Fig. 3.5), and a further 50% decrease in *B. glaciale* abundance from June to August in the large scale IYGPT survey (Table 2.10) indicate that fewer large individuals were migrating into the upper 200 m than had in April or June. An absence of individuals < 25 mm in IYGPT samples, in comparison to their abundance in the Tucker trawl, again demonstrates that a substantial fraction of the population was not collected by the larger trawl.

Distribution of *B. glaciale* with depth as illustrated by Tucker trawl sampling was similar among the surveys. It occurred mainly between 50 or above and 100 m depths at night, and during the day at depths of 450-600 m or more. Numbers in Tucker trawl samples increased in both June and August due to the appearance of fish spawned that year. Fewer large (>32 mm) *B. glaciale* were captured in June and August than April, due to decreasing abundance of those individuals older than one year.

Ceratoscopelus maderensis

Only 16 individuals were captured in Tucker trawl tows in April (Fig. 3.6). At night, they were collected only at 50 m (7 fish/tow, 18-52 mm). Two day tows caught single individuals at 400 and 600 m (38 and 26 mm, respectively).

In June, catches at night increased to 263 fish/tow at 50 m depth. The maximum fish size and range was less at this depth (12-19 mm) than observed in April and all specimens were postlarvae, except one 19 mm

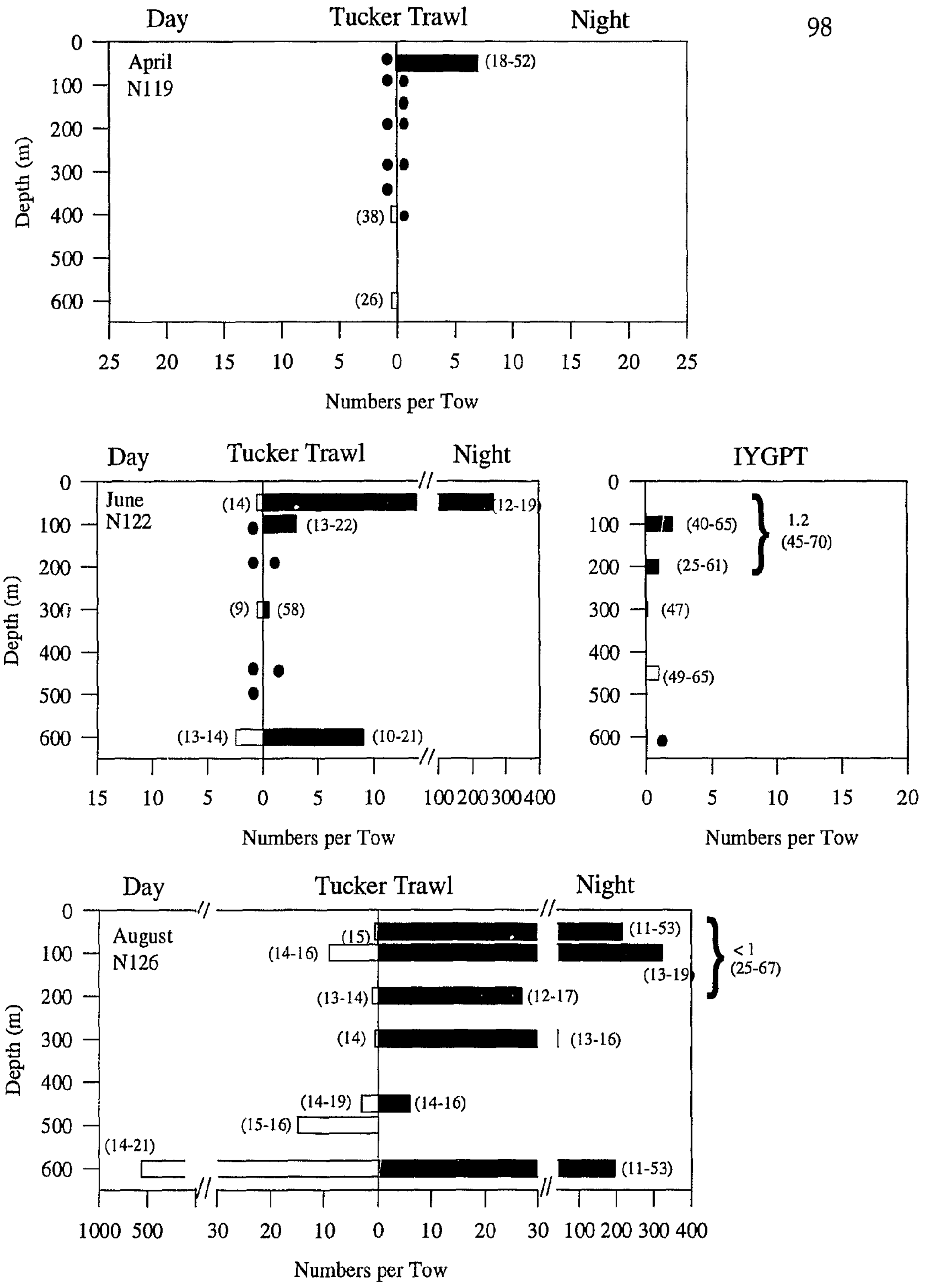


Figure 3.6. Day and night vertical distributions of *Ceratoscopelus maderensis* (mean no. /tow) in April, June and August Tucker Trawl samples and adjusted catch rates in June IYGPT tows. Length range shown in brackets. Inclusive brackets show adjusted stepped oblique IYGPT catch in June and August. ● - none caught.

postmetamorphic individual. Abundance was bimodally distributed at night; the highest catch rate occurred at 50 m but some postlarvae and one juvenile were collected at 600 m. A few were also taken at 100 m and a single specimen at 300 m. Day tows only captured a few postlarvae: single occurrences at 50 and 300 m, and 3 fish/tow at 600 m.

In August, 96% of the individuals in the night tows at 50 m appeared to have recently metamorphosed to the adult phase (15-25 mm) while 83-100 % of individuals at depths 100-450 m were still predominantly postlarvae (12-17 mm). Abundance was bimodally distributed with night catches at 600 m comparable to those at 50 and 100 m. The ratio between postlarvae and adults at 50 and 600 m was approximately equal. Largest day catches occurred at 600 m (565 fish/tow), where about 28% of the catch were postlarvae, but a few postlarvae and adults were captured at all depths. Animals older than one year were very rare as the only large fish collected were a few 53 mm individuals at 50 and 600 m depths at night.

IYGPT tows in June indicated that larger (>25 mm) *C. maderensis* were present but not abundant at all sampled depths (Fig. 3.6). Higher IYGPT catches at night but a similar size range to day catches (25-65 mm and 47-65 mm, respectively), suggest that most of the population may migrate deeper than 600 m during the day. In August, the single three-step IYGPT capture of 23 individuals (adjusted catch rate < 1 fish/tow, 25-67 mm length) was comparable to Tucker trawl collections, confirming that few *C. maderensis* older than a year were present.

Numbers of C. *maderensis* increased between April and August, due to the appearance of fish spawned that year. Numbers of older individuals decreased from April to June. Night time distribution became increasingly bimodal from June to August, with concentrations at 50-100 m and 600 m depths. Individuals < 19 mm did not regularly migrate as they were found at all depths both day and night in August. However, catch rates were an order of magnitude less at depths < 300 m during the day than they were at night.

Cyclothone

In April, *Cyclothone* spp. was captured at night only at 400 m, but no deeper depths were sampled (Fig 3.7). In the day, numbers increased with towing depth from 350 to 500 m, and were approximately equal at 500 and 600 m. In June, *Cyclothone* spp. was collected during the night from 450 and 600 m depths, and during the day at 600 m, only. Numbers of fish collected at 600 m during the day and night were about equal. In August, the night and day distribution with depth was similar; *Cyclothone* spp. first occurred in the 300 m samples and increased in abundance with towing depth. Day tows at 600 m caught 126 fish/tow, or about three times as many animals as the night tows. No *Cyclothone* spp. were collected in the IYGPT tows in June or August.

Comparing distribution of catches with depth among surveys, *Cyclothone*

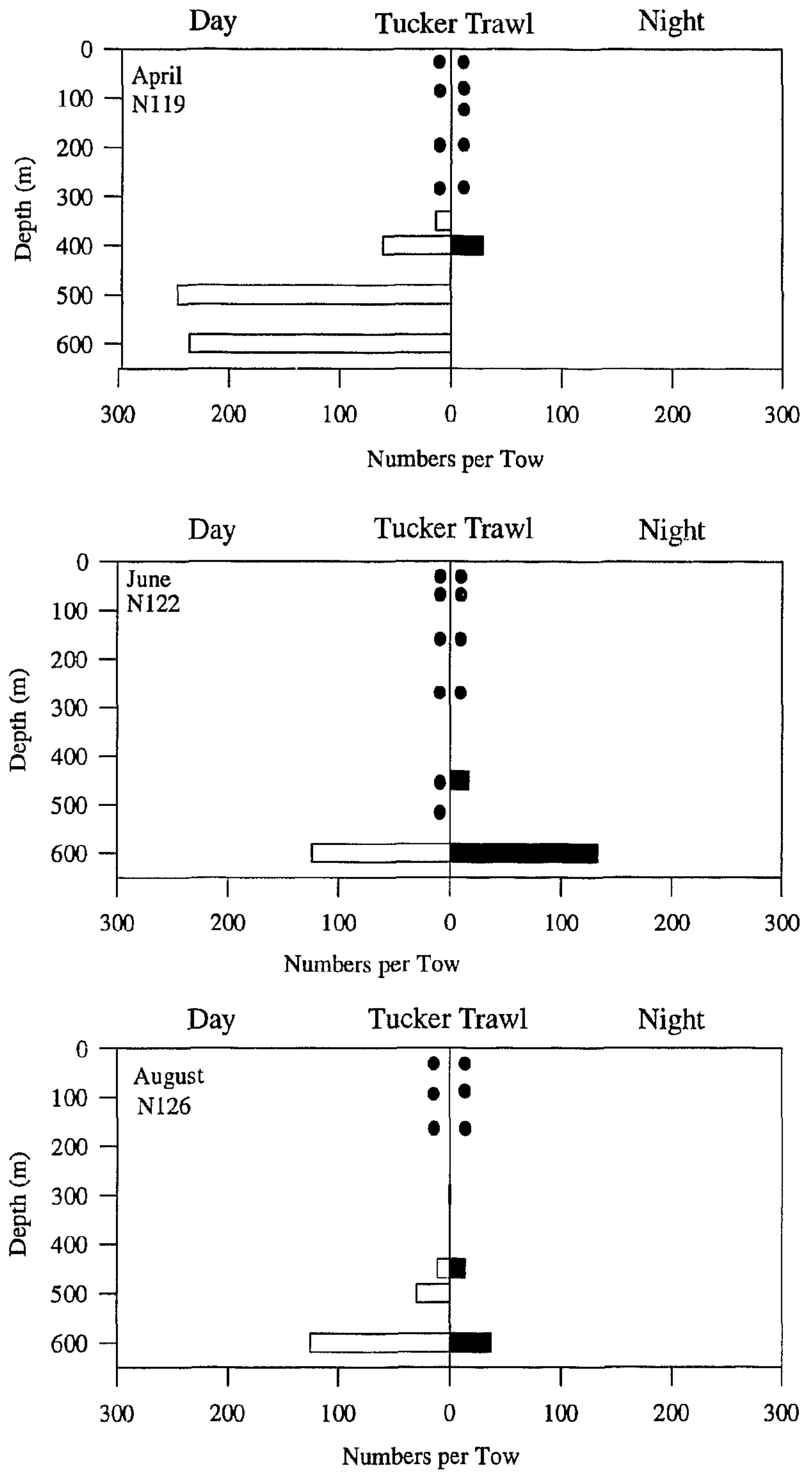


Figure 3.7. Day and night vertical distributions of *Cyclothone* spp. (mean no./tow) in April, June and August Tucker trawl samples (none caught in IYGPT tows. ● - none caught

was not captured at depths shallower than 300 m. Sampling depth was not deep enough to cover the depth range of this species.

Notolepis rissoi

All but one *N. rissoi* caught in the Tucker trawl were postlarvae < 61 mm. In April at night, *N. rissoi* doubled in abundance from 11 fish/tow at 50 m to 20 fish/tow at 150 m, and no individuals were captured below 200 m (Fig. 3.8). No day time zone of abundance was discernible since only a few individuals were collected and these came from almost all depths sampled. Similar size ranges were caught in night (21-53 mm) and day (26-51 mm) samples. In June, only nine fish were collected in 22 tows. The largest catch (n=3) occurred at 100 m at night and none were taken below 200 m. The largest catches and widest size range (17-63 mm) of *N. rissoi* in Tucker trawl samples occurred in August. Maximum abundance at night was again at 100 m (28 fish/tow). Size stratification by depth was conspicuous: the length range of individuals captured at 50 and 100 m = 17-31 mm, and at 200 m and deeper = 32-63 mm. In the day highest abundance occurred at 100 m. Day time length ranges (17-41 mm) were similar to those from night tows at the same depth (17-31 mm).

Abundance in the IYGPT samples in June was low. The two gears sampled different size ranges since the IYGPT caught both postlarvae and adults (44-109 mm). Capture of *Notolepis rissoi* during the day by the IYGPT at

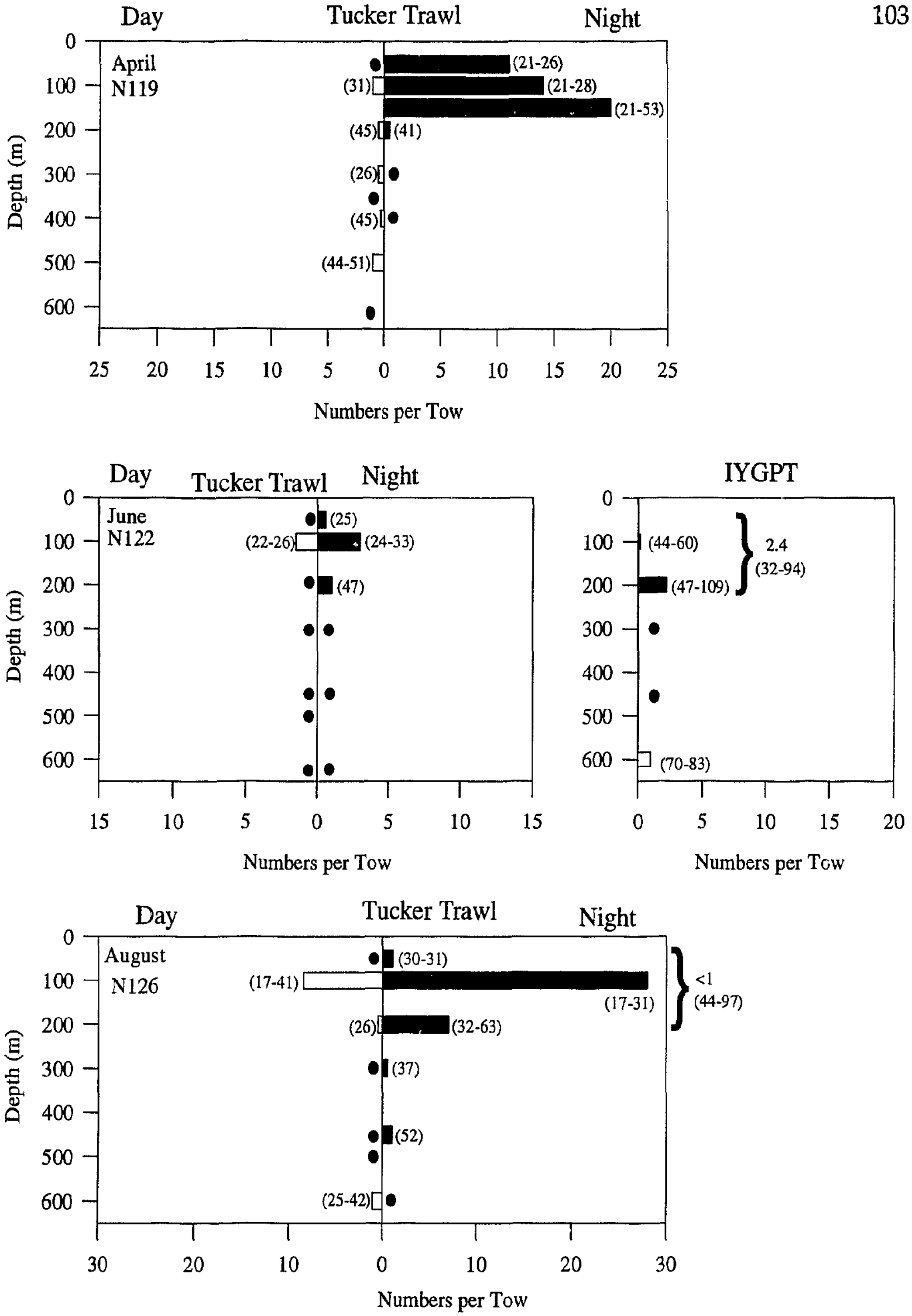


Figure 3.8. Day and night vertical distributions of *Notolepis rissoi* (mean no./tow) in April, June and August Tucker Trawl tows and adjusted catch rates in June IYGPT tows. Length range (mm) shown in brackets. Inclusive brackets show stepped oblique IYGPT catches rates in June and August.● -none caught.

600 m but not 300 or 450 indicates that 600 m marks the upper day time limit of individuals > 50 mm. In August, large *N. rissoi* were very low in abundance since only nine individuals (adjusted catch rate of < 1 fish/tow, 44-97 mm length) were collected in the IYGPT stepped oblique tow.

Notolepis rissoi decreased in abundance from April to June, and overall numbers were highest in August. At night, the depth at which abundance was highest was deeper in April (150 m) than in June and August (100 m), however, there was also evidence of size stratification with depth, at least in the Tucker trawl samples from August. Day time catches were always low, except at 100 m in August. Some individuals < 45 mm were collected from the upper 200 m during the day in all three months but night catches were always several times higher. Fish > 50 mm migrated to day time depths greater than 600 m. Larger animals were caught by the IYGPT (32-109 mm) than the Tucker trawl (21-51 mm).

Lobianchia dofleini

In April *L. dofleini* occurred only at 50 m depth in low numbers at night (3 fish/tow, Fig. 3.9). In June at night catch rates were low except at 50 m (39 fish/tow). The single individual at 600 m was not a contaminant since no *L. dofleini* were caught in the preceding tow (a 600 m day tow). In August, the zone of maximum abundance was at 100 m; catch rate there (31 fish/tow) was several times greater than at 50 or 200 m. Size stratification with depth was

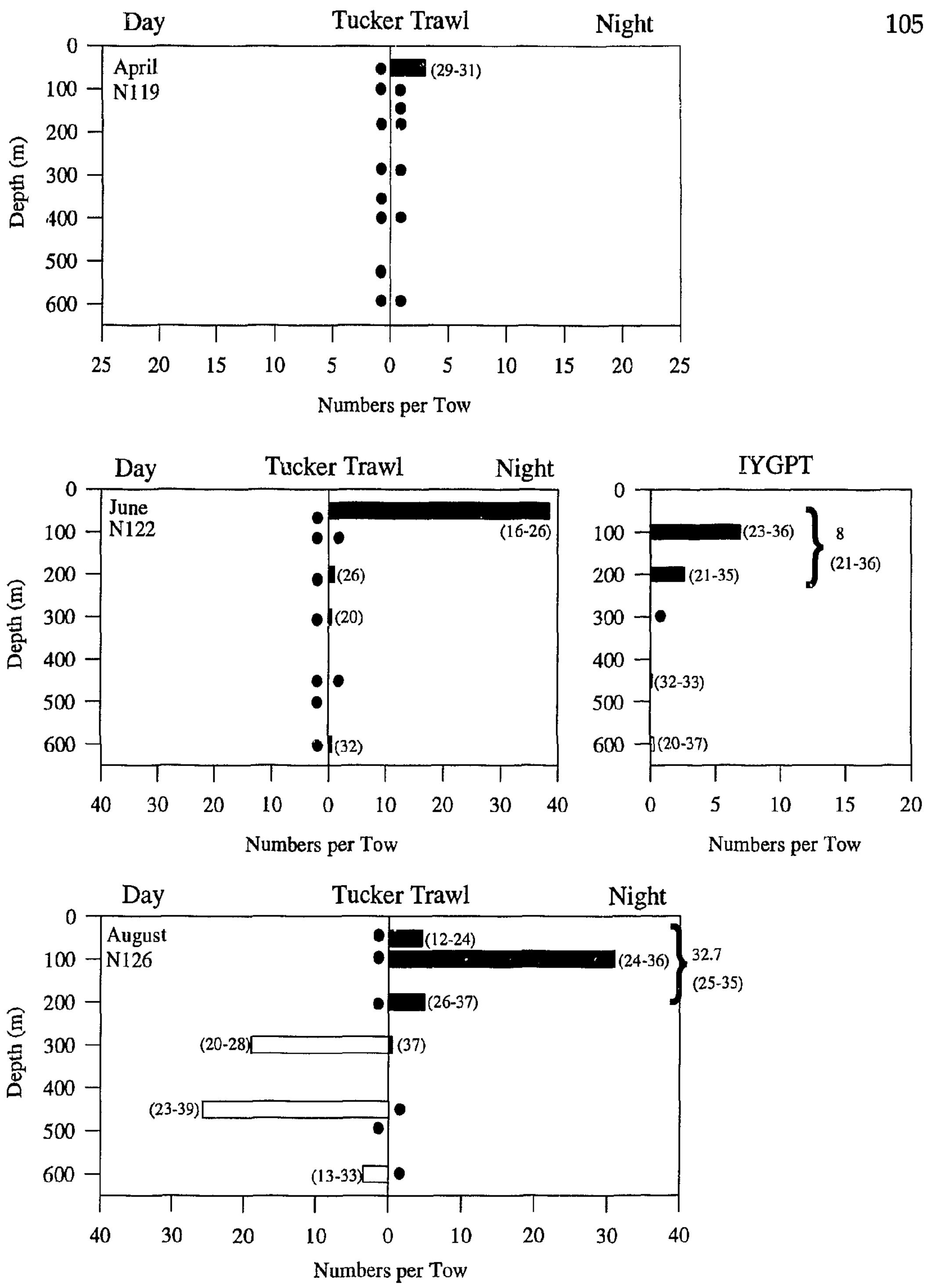


Figure 3.9. Day and night vertical distributions of *Lobianchia dofleini* (mean no./tow) in April, June and August Tucker Trawl tows and adjusted catch rates in June IYGPT tows. Length range (mm) shown in brackets. Inclusive brackets show stepped oblique IYGPT catches rates in June and August.● -none caught.

indicated by a smaller size range of animals at 50 m (12-24) than at 100-200 m (24-37). Catch rates at greater depths were negligible. In day tows in August *L. dofleini* was captured only at depths greater than 200 m. The zone of maximum abundance was at 450 m, the catch rate there being comparable to the catch rate at 100 m at night, whereas the numbers of fish taken at 500 or 600 m were very low. Size range between day and night samples was similar (day:13-34 mm, night:12-34 mm). A shift in the nighttime depth of maximum abundance from 50 to 100 m and size stratification, with larger individuals occurring at greater depths, were also observed in *L. dofleini* in the Sargasso Sea between June and August-September (Karnella 1987).

The stepped oblique IYGPT tow caught fewer animals than shallow night Tucker trawl tows in June, but comparable numbers in August (Fig. 3.9). In June, the IYGPT night tows caught larger fish (21-36 mm) than the Tucker trawl at depths < 200 m (16-26 mm), while in August, the size range in the 100 and 200 m night Tucker trawl tows (24-36 mm) was similar to that in the IYGPT tow (25-35 mm). Increased catch rates in the IYGPT between June and August are due to the larger size of animals present in the latter month. In the Sargasso Sea, Karnella (1987) reported that 80% of the *L. dofleini* population captured in June were juveniles with body lengths of 10-24 mm, whereas the same proportion were subadults (19-36 mm) in August. Assuming that the Slope Water population has similar growth patterns to that of the Sargasso Sea, most animals would be too small in June to be retained by the IYGPT.

Lobianchia dofleini increased in abundance in Tucker trawl catches from April to June and August, due to increasing numbers of small (12-28 mm) animals. In August, the size range at 100-200 m in the Tucker trawl was the same as in the IYGPT because this species is size stratified by depth at night. There were seasonal changes in its vertical distribution as the night time depth of maximum abundance deepened from 50 m in June (38 fish/tow) to 100 m in August (32 fish/tow). Failure to captured any animals in day time Tucker trawl tows in April and June cannot be explained with the present data.

Hygophum hygomii

In April, *H. hygomii* was only collected at three depths in the day: 8.5 fish/tow at 350 m, and < 3 fish/tow at 400 and 500 m (Fig. 3.10). In June, *H. hygomii* was collected at two depths: at night at 50 m (4 fish/tow), and 17 fish/tow in the day at 450 m. In August at night, *H. hygomii* occurred at 50 m (4.5 fish/tow), and as < 2 fish/tow at 100 m, and at 400 and 600 m in the day (Fig. 3.10).

The low average catch of *H. hygomii* in the broad-scale IYGPT survey in April (adjusted rate of < 1 fish/ tow, Table 2.10, Chapter 2), as well as the moderate quantities captured in day Tucker trawl tows, suggests that the absence of this species in the night time Tucker trawl tows was due to low abundance rather than avoidance of the smaller trawl. The 50 m tow may have been too deep to sample the population since this species is neustonic at night (Nafpaktitis et al. 1977; Linkowski 1996). In June, the IYGPT and Tucker trawl were equally effective in the day, based upon similar catches at 450 m. Comparison of catch rates in the Tucker trawl and concurrent June and August IYGPT tows show that the IYGPT caught about twice as many fish at depths of 200 m or less (Fig. 3.10). This may be the result of the IYGPT sampling the surface layer as it was retrieved. Overall, adjusted catch rates of the broad-scale IYGPT surveys in June (5.3 fish/tow) and August (6 fish/tow; Table 2.10) were very similar to the catch rate of the Tucker trawl at 50 m (4 and 5 fish/tow, respectively), indicating patchy distribution. In both June and August, a wider size range was sampled by the IYGPT (21-63 mm) than the Tucker trawl (31-52 mm).

Between April and June, numbers of *H. hygomii* doubled, and the day time depth of maximum abundance increased from 350 to 450 m. Maximum numbers at night were between 4 and 5 fish at 50 m in June and August. These numbers were less than concurrent IYGPT tows which caught greater numbers of individuals of a greater size range.

3.4 Discussion

3.4.1 Vertical distribution of the fauna

Most of the mesopelagic fauna was concentrated in the upper 200 m at night, and at 500 to 600 m (or more) in the day. This night time depth of concentration is in agreement with Sameoto's (1982) observation of an acoustic

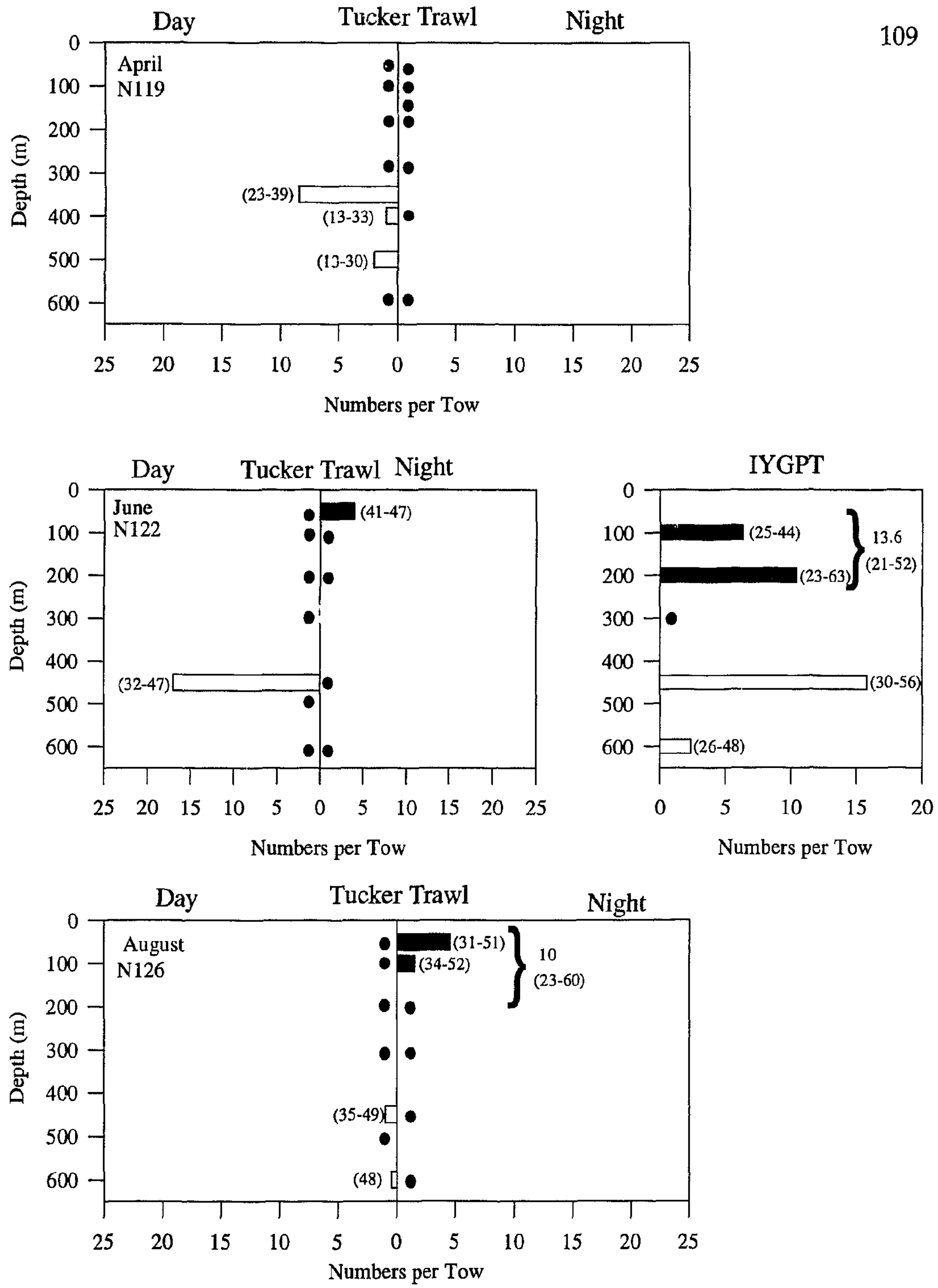


Figure 3.10. Day and night vertical distributions of *Hygophum hygomii* (mean no./tow) in April, June and August Tucker Trawl tows and adjusted catch rates in June IYGPT tows. Length range (mm) shown in brackets. Inclusive brackets show stepped oblique IYGPT catches rates in June and August.● -none caught.

scattering layer at 75-125 m in the Slope Water, which he attributed to a concentration of myctophids, and Halliday (1970) who reported *B. glaciale* (the most abundant member of the fauna) to be concentrated between 45 and 90 m at night. Vertical distribution studies in other regions have shown that mesopelagic fish species have an extensive vertical range with many species occupying depths above 250 m at night, and between depths of 400 and 1200 m in the day (Nafpaktitis et al. 1977; Karnella 1987; Brooks and Saenger 1991). The vertical range of sampling in this study was broad enough to sample most species within their day and night depth ranges. However, the night zone of highest abundance of neustonic species (e.g. *Myctophum, Symbolophorus,* and *Hygophum* spp.; Nafpaktitis et al. 1977; Gartner et al. 1989) was not sampled. The maximum sampling depth of 600 m was also too shallow to sample the entire daytime depth range of some species.

Comparisons of individual vertical distributions between the Slope Sea and other oceanic regions (Northeast Atlantic: Badcock 1970; Merrett and Roe 1974; Badcock and Merrett 1976, 1977; Kinzer 1977; Kawaguchi and Mauchline 1982; Roe and Badcock 1984; Zelck and Klein 1995; Mediterranean: Goodyear et al. 1972; Northwest Atlantic: Halliday 1970; Craddock et al. 1992; Sameoto 1988; Janssen et al. 1992; off Bermuda in the Sargasso Sea: Gibbs et al. 1971; Karnella 1987; broad scale surveys of the North Atlantic: Rofen 1966; Nafpaktitis et al. 1977; Linkowski 1996) indicate general agreement on the depth range covered during vertical migration (Fig. 3.11). *Cyclothone* spp. were

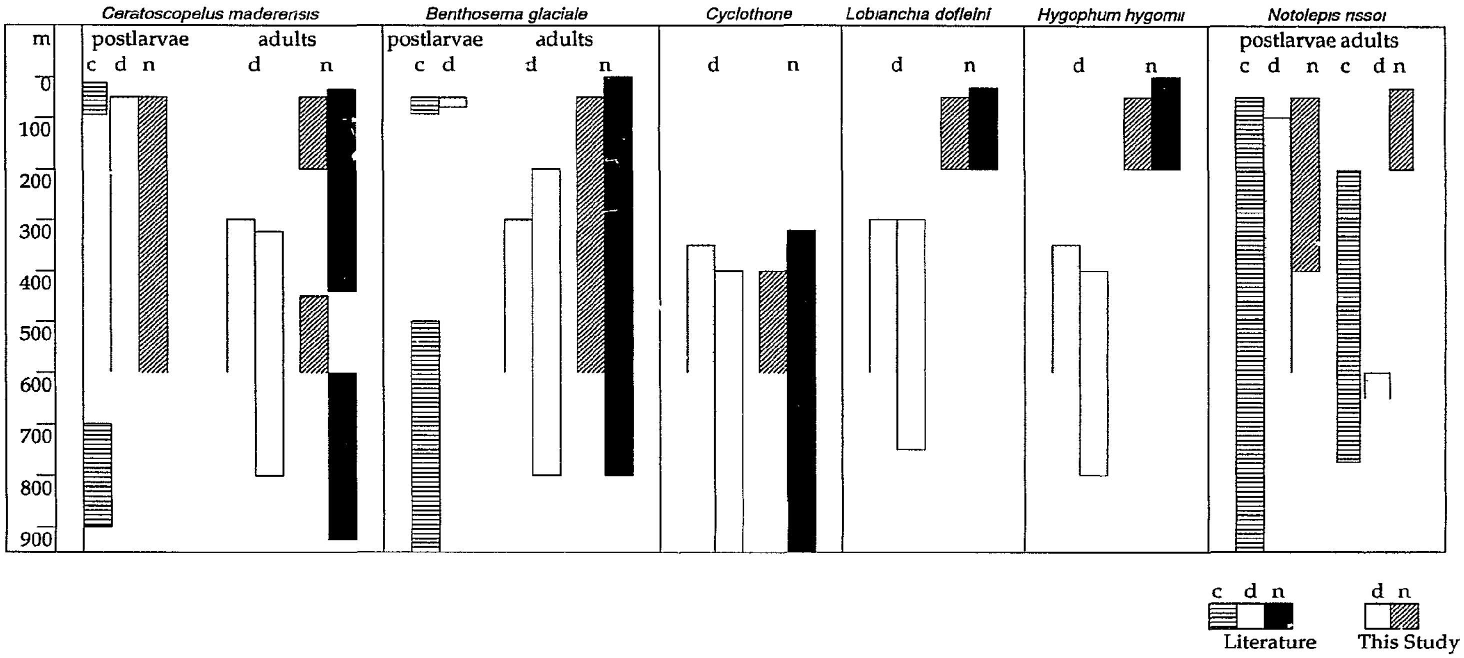


Figure 3.11. Comparative depth distributions of six mesopelagic fish species between the Slope Sea and other regions of the Atlantic Ocean and Mediterranean Sea (c=combines day/night; d-day; n-night) Open bottoms to boxes indicate that sampling did not extend deep enough to define lower distributional limit.

the only species examined which did not vertically migrate. Only a portion of the collective depth range of these species was sampled as it extends from 400 m to deeper than 1000 m (Fig. 3.11).

3.4.2 Comparisons between the IYGPT and Tucker trawl

Comparison of species collected by the two trawls indicates that the IYGPT is an effective qualitative sampler of the fish fauna inhabiting the mesopelagic zone of the Slope Sea. In spite of its smaller mesh size, the Tucker trawl did not collect any species that were not also sampled by the IYGPT, with the exception of a single specimen of the stomiatoid, *Thysanactis dentex,* which is a rarely occurring species (Morrow and Gibbs 1964).

Many characteristics of the mesopelagic fauna represented in the samples collected by the Tucker trawl and the IYGPT (Chapter 2) are similar. Both trawls sampled a mesopelagic fauna dominated by the families Myctophidae and Gonostomatidae. Four of the top six species in Tucker trawl samples (*B. glaciale, C. maderensis, L. dofleini,* and *N. rissoi*) were among the six most abundant species sampled by the IYGPT. However, two highly ranked species in Tucker trawl samples, *Cyclothone* spp. (second) and *Diogenichthys atlanticus* (sixth), were ranked eighth and twenty-sixth, respectively, in IYGPT samples. The low abundance of *D. atlanticus* in IYGPT tows was attributed to its small size (Chapter 2). Differences in relative abundance of *Cyclothone* spp. are partially due to the distribution of sampling effort with depth by the two trawls. *Cyclothone* spp. occurred mainly in the Tucker trawl samples collected from depths below 400 m; 25% of all tows with this net were at or below this depth, compared to 20% of all IYGPT tows. Also, the total absence of *Cyclothone* spp. in the 600 m IYGPT tow in June while it was abundant in Tucker trawl tows at the same depth indicate that *Cyclothone* spp. is too small to be retained by the meshes of the IYGPT. Tows at comparable depths by the two trawls demonstrate that *D. atlanticus* is also too small to be proportionally represented in IYGPT samples. An average of 70 *D. atlanticus*/tow were collected by the Tucker trawl at 50 m in August compared to none in the stepped oblique IYGPT tow.

Comparing the catch rates of abundant species in the two trawls provides an evaluation of relative abundance of species in the Slope Water which were determined mainly from stepped oblique IYGPT tows (Chapter 2). Most of the catch in the stepped oblique tow was probably collected in the 100 and 50 m steps while the 200 m step contributed larger individuals of species such as *N. rissoi* and *B. glaciale.* The IYGPT does not appear to have underestimated numbers of *N. rissoi, H. hygomii,* and *C. maderensis* (except postlarvae), since it was more effective than the Tucker trawl in collecting these species. Comparison of catch rates for *L. dofleini* suggested that the effectiveness of the IYGPT increased between June and August, as the size range increased. Underestimation of *Cyclothone* spp. was inevitable, given the mesh size of the trawl and sampling programme. Overall, the Tucker trawl was much less efficient than the IYGPT at capturing *B. glaciale* > 32 mm, but much more effective in capturing individuals < 32 mm.

Catches of *B. glaciale* in the two trawls indicate a decrease in the abundance of large (> 32 mm) individuals between April and the summer and fall surveys at depths between the surface and 600 m. Relative and absolute abundance of *B. glaciale* were shown to decrease between June and October in stepped oblique (night) IYGPT tows (Chapter 2). In Tucker trawl tows conducted in June and August, only one large individual occurred at depths < 400 m and the numbers at greater depths were low, in contrast to the numbers captured at corresponding depths in April.

This reduction in the numbers of age-1+ *B. glaciale* could be caused by their disappearance from the WSW due to migration or death, or that fewer vertically migrate at night from daytime depths to the upper 200 m in the summer. The abundance of *B. glaciale* in deep (> 350 m tows) day time IYGPT tows did not decrease between the winter and summer standard surveys (data not shown). Evidence from other sources indicates that the proportion of age-1+ individuals vertically migrating in the WSW is variable. Sameoto (1988) observed that most *B. glaciale* migrated from depths of 300-800 m in the day to depths < 200 m at night in April through July and in one of two October surveys. In the other survey, a large proportion of the population remained at daytime depths during the night, which he attributed to a warm (18 °C) water mass at the surface. Although fish size with depth is not indicated, at least

50% of the fish captured in that survey were > 30 mm and age-1+. Olson and Backus (1985) reported that age-1+ *B. glaciale* did not vertically migrate in the WSW south of the study area (although some proportion of age-0 fish did). In the present study, some age-1+ individuals always vertically migrated, since animals with lengths of 60-69 mm were captured at night at depths < 200 m in all the standard IYGPT surveys. The observed decrease in abundance of age-1+ *B. glaciale* in the shallow, night tows appears to be due both to decreased vertical migration and abundance.

Chapter 4: Spatial distributions of mesopelagic fish species in the Slope Sea off Atlantic Canada

4.1 Introduction

Midwater fish surveys in the Slope Sea adjacent to Nova Scotia indicate that the species composition of the mesopelagic fish fauna is not homogenous. Samples taken closest to the Scotian Shelf were dominated by species otherwise found in subarctic and temperate locations while the abundant species in samples from seaward locations tended to have more subtropical or tropical distributions (Backus et al. 1970, 1977; Chapter 2).

Studies by Jahn and Backus (1976) and Backus and Craddock (1982) related differences in faunal composition to the three water masses present off Atlantic Canada: Slope Water, Gulf Stream and Sargasso Sea. Each water mass was characterized in terms of its species diversity and dominant species. The implications of these conclusions were that the species composition within any one water mass would be distinct and relatively homogenous, with faunal disjunctions occurring at or near the boundaries of water masses. McKelvie (1985a) re-evaluated these conclusions using data from more intensive midwater surveys which, in addition to the Slope Water and Gulf Stream, sampled the cold water mass lying adjacent to the continental shelf (Labrador Slope Water) which is derived from the Labrador Current (Newfoundland Basin). He disagreed that discrete faunal groups occurred, arguing that his results were more consistent with a gradation between northern and southern faunas originating from the Newfoundland Basin and Gulf Stream, respectively, and thus that the Slope water is a transition zone or ecotone and its fauna a mixture of species originating from the bordering regions.

The purpose of this chapter is to examine horizontal patterns in mesopelagic fish species distributions in the Slope Sea. Objectives of this chapter are: to identify major patterns in species distributions and any variations in these patterns spatially and seasonally; determine if the observed variations are gradual, or abrupt and therefore indicative of discrete faunal zones; and relate species distributions to the large-scale hydrographic fronts. Possible impact of the surface layer on species distributions is also considered by relating temperatures of the subsurface and surface water masses to species composition.

4.2 Methods

4.2.1 Data collection

Mesopelagic fish were collected by the MV *Alfred Needler* on six cruises conducted by the Department of Fisheries and Oceans in the slope region off Nova Scotia between February 1988 and August 1989 (Table 4.1). Fishing stations (or sites) were located 10 to 15 miles apart on transects running south of the 1000 m depth contour (Fig. 4.1a-f). An International Young Gadoid Pelagic Trawl (IYGPT) was fished at night in a standardized stepped-oblique

Table 4.1. Designations, dates and number of samples collected on the six standard mesopelagic cruises.

Cruise	Date	Number of samples
N096	Feb 17-Feb 25/88	18
N110	Oct 18-Oct 26/88	34
N112	Nov 30-Dec 8/88	34
N119	Apr 12-Apr 20/89	9
N122	June 6-June 15/89	13
N126	Aug 10-Aug 18/89	18

tow consisting of three consecutive 10 minute steps at 200, 100 and 50 m depths (Chapter 2). Sampling intensity per cruise was variable with the highest sampling frequency occurring in October (N110) and the lowest in April (N119, Table 4.1). Sample processing and oceanographic data collection are described in Chapter 2.

4.2.2 Ordination of sites

Detrended Correspondence Analysis (DCA, Hill and Gauch 1980), as implemented by the computer program DECORANA (Hill 1979a), was chosen to ordinate fishing stations based upon their species composition. Multi-dimensional scaling (MDS) has been recommended for ecological data (Field et al. 1982), but it requires subjective choices on the distance measure and the appropriate number of dimensions, and it is not as useful in evaluating the effectiveness of the chosen classification method. Principal Component Analysis (PCA) was also rejected because of an inherent assumption of a linear relationship between species abundance data and environmental variables (Gauch 1982; ter Braak 1987; ter Braak and Prentice 1988). DCA was considered more appropriate than PCA because sampling was assumed to have occurred over a large enough area to encompass the entire distribution of some species. In DCA, species are assumed to exhibit unimodal response curves to environmental gradients by appearing, rising to some maximum abundance and then disappearing along the gradient. In the ordination, a

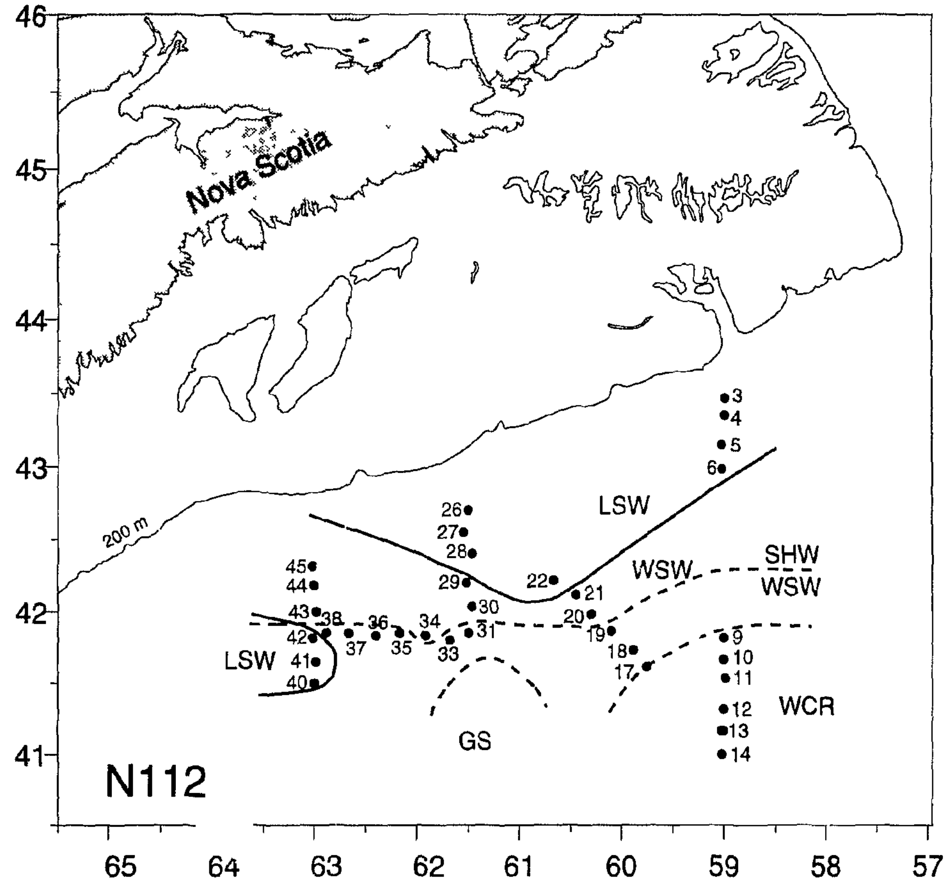


Figure 4.1 Sampling locations and the positions of the hydrographic fronts during six mesopelagic surveys of the Slope Sea in seasonal progression from December to October. Solid and dashed lines indicate subsurface and surface hydrographic fronts, respectively, between Labrador Slope Water (LSW) and Warm Slope Water (WSW), and between WSW and Shelf Water (SHW), Gulf Stream (GS) or a ring (WCR). a. December (cruise N112).

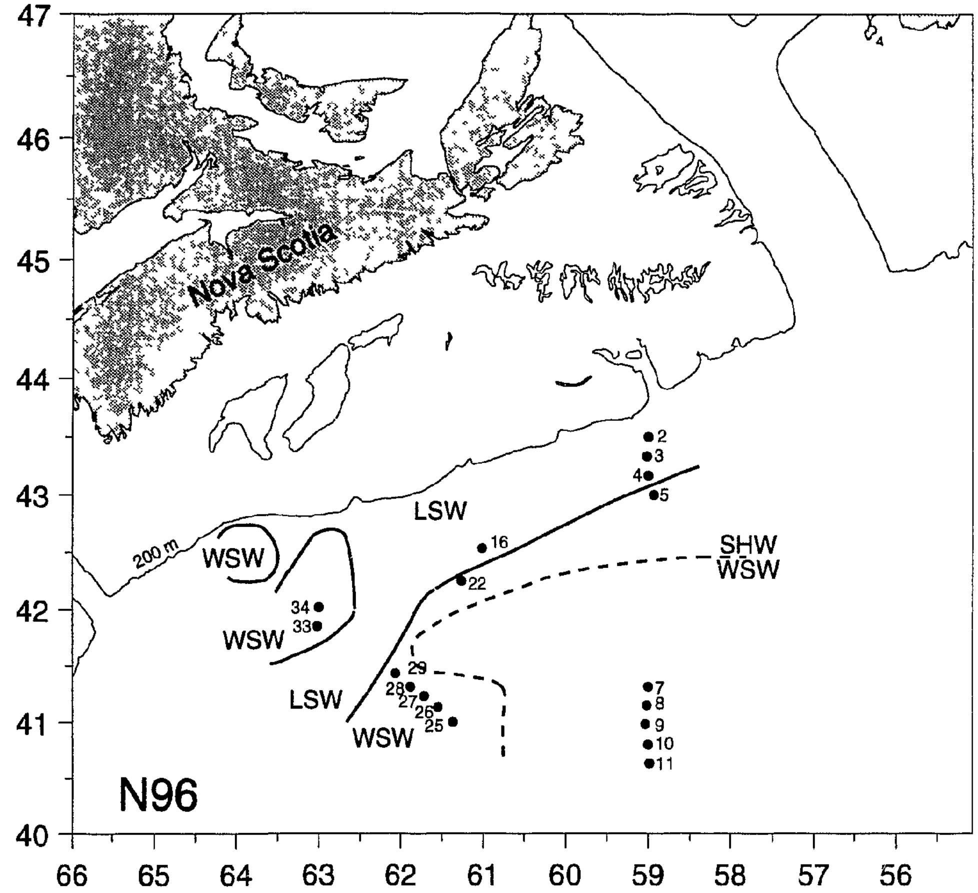


Figure 4.1 (cont.) b. February (N096).

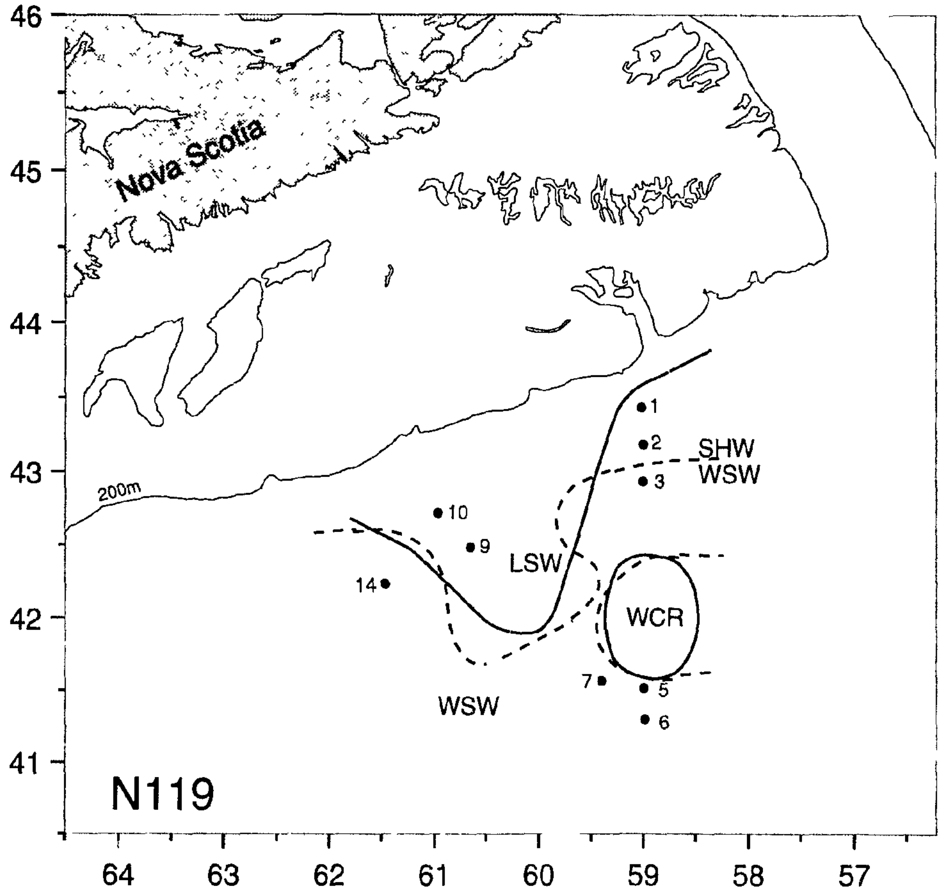


Figure 4.1 (cont.) c. April (N119).

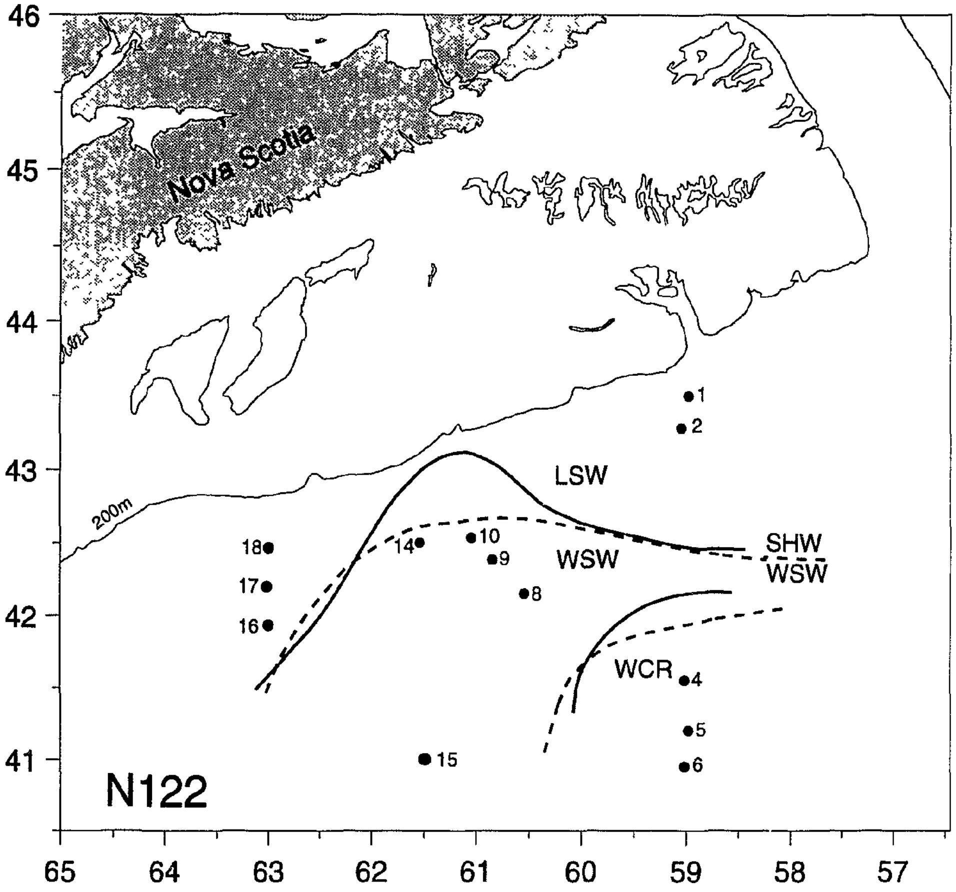


Figure 4.1 (cont.) d. June (N122).

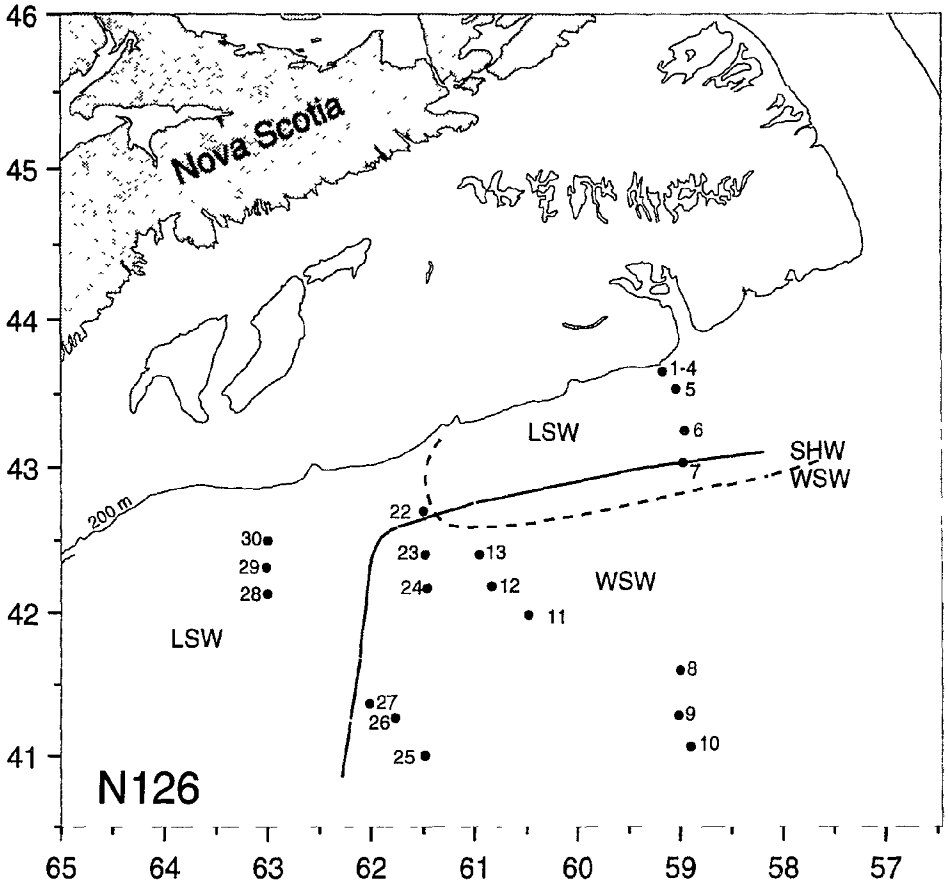


Figure 4.1 (cont.) e. August (N126).

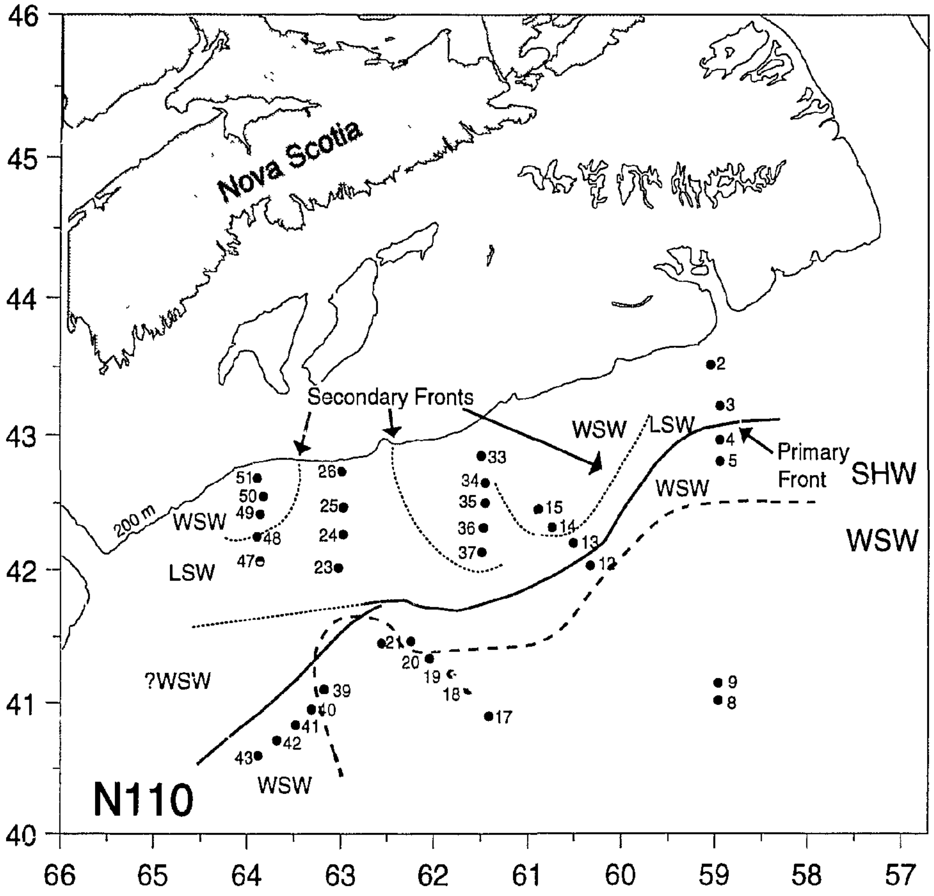


Figure 4.1 (cont.)f. October (N110). Seaward subsurface fronts of cool WSW occurring along shelf slope are labelled 'secondary fronts'.

given species occurs over a distance of four units, with each unit equivalent to one half-change or standard deviation (Gauch 1982). Theoretically, stations four units apart on a DCA axis have no species in common because sites are scored on the basis of their average species scores. Five of the six surveys had gradients longer than the minimum of two units required for DCA to work well (Gauch 1982; Peet et al. 1988; ter Braak and Prentice 1988). Strong agreement between DCA and the classification method in analyses of the April survey indicates that the short gradient (1.8 units) did not affect the success of the ordination of this survey.

Simultaneous ordering of stations and species is an important feature of DCA which aids in interpretation of ordination results. Species are placed nearest the sites at which they are the most abundant, so species are located on the axis where they show a preference for the environmental conditions associated with that end of the gradient. Ubiquitous and rare species are uninformative as they tend to be positioned near the origin and at the extreme ends of the axis, respectively (Gauch 1982). A short gradient occurs when most species are shared by all sites. Only ordination diagrams of sites were examined here, but the basis for species placement is pertinent to the explanation of the classification method (TWINSPAN) which follows.

An Eigenvalue is a measure of the relative importance of an axis. The first axis has the highest eigenvalue and axes with eigenvalues less than 10 %

of the first are unimportant. Eigenvalues are also a measure of the degree of correlation between species and site scores (ter Braak 1987).

DCA was developed from Correspondence Analysis (CA) to compensate for the 'arch effect' and distortion of relative distances along the axes which can occur in CA ordinations. The computer program DECORANA removes tne arch by dividing the first axis into segments and then adjusting the second axis scores within each segment to have a mean zero value. Compression of the endpoints of the axes are corrected through non-linear rescaling, which expands or contracts segments along the species ordination axis so that species turnover occurs at uniform rate (Gauch 1982). Detrending by segments has been criticized because ecologically meaningful data could be inadvertently destroyed (Pielou 1984; Wartenberg et al. 1987; reviewed by Palmer 1993). However, Peet et al. (1988) argue that this is a minor issue, in view of the usefulness of detrending for interpretation of the ordination.

Species occurring only once within a survey were removed. Abundance data were log-transformed (ln(x+1)) to decrease the effect of very abundant species on the ordination (Gauch 1982). Rare species were not downweighted, axes were not rescaled and 26 segments (the default) were used in detrending the second axis. Axes scores were correlated with surface and 200 m water temperatures, surface salinity and bottom depth as an indicator of distance from shore.

4.2.3 Classification of sites and species

Sites and species were classified using Two Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979b), a divisive polythetic method. TWINSPAN orders sites on the first axis of a correspondence analysis and then divides the axis near its midpoint into negative (left) and positive (right) sides. The division is refined by a reclassification using species which show a preference for one side or the other (van Tongaren 1987). Successive divisions of the axis form a hierarchical site classification which is then used to develop a species classification. The 'two classifications are then used together to obtain an ordered two-way table that expresses the species' synecological relations as succintly as possible' (Hill 1979b). Species (rows) are placed near the top of the table if they are more abundant at sites (columns) ordered to the left side of the table, species near the bottom are more abundant at sites on the right side. TWINSPAN is similar to DCA in placing ubiquitous species in the middle of the two-way table and rare or outlier species at the very top or bottom. Abundance categories called pseudospecies are used instead of actual abundance data. The more abundant a species is at a site, the more pseudospecies it has. Six levels were chosen: 1 (1-4 individuals); 2 (5-9 ind.); 3 (10-49 ind.); 4 (50-99 ind.); 5 (100-499 ind.) and 6 (> 500 ind.).

Results from the TWINSPAN classification were compared to the more traditional approach of an agglomerative, hierarchical clustering method.

Similarities between station pairs were measured by the independent form of the Percentage Similarity index (PSi):

$$PS_i = 1 - 0.5\sum |p_{ij} - p_{ik}| = \sum \min(p_{ij}, p_{ik})$$

where p_{ij} and p_{ik} are the proportion of species i in the total catch at sites j and k, respectively. This index is unaffected by differences in numbers of animals or diversity between samples (Wolda 1981; Kohn and Riggs 1982) and accurately reflects similarity between samples (Bloom 1981). It has been used frequently in other studies on mesopelagic fish community studies for between sample or between region comparisons (Jahn and Backus 1976; Barnett 1983; 1984; Brandt 1983; Griffiths and Wadley 1986). Boesch (1977) criticises the index for being too sensitive to abundant species. Similarities between stations are largely determined by the number of shared and abundant species, because dominant species contribute more than rare species to a station's score. However, some sensitivity to dominant species was desirable as a contrast to TWINSPAN, which emphasizes whole community composition (Gauch and Whittaker 1981) and might be overly influenced by rare species. Data were square-root transformed prior to calculating PSi to decrease the effect of abundant species (van Tongaren 1987). Within each cruise, species occurring only once were removed. Cluster dendrograms were calculated from the similarity matrices of each cruise using average linkage. Trial runs clustering Canberra-Metric and Bray-Curtis dissimilarity matrices of samples from one of the cruises produced identical site groups as PSi.

4.2.4 Oceanographic conditions

The oceanographic data collected during the six cruises and their interpretation are described in Halliday et al. (1995). Surface fronts between SHW and WSW were determined from temperature data for consistency, although salinity data appeared more appropriate for the August (N126) survey. Figure 4.1a-f shows the positions of the sites sampled relative to subsurface fronts (at 200 m) between Labrador Slope Water (LSW) and Warm Slope Water (WSW) and between WSW and Gulf Stream (GS) or a Warm Core Ring (WCR), and the surface fronts between WSW and Shelf Water (SHW), GS or WCR. A WCR was sampled on the southern end of the easternmost transect in December and June (and was also adjacent to stations sampled there in April) and GS water was also present near the southernmost stations sampled in August and October. Cold LSW always occurred on the northern end of the easternmost transect, and on parts of the western transects in all months except August. Interleaving between layers of WSW and LSW was occurring in June (N122) at sites 16-18 and on several transects in October (indicated as secondary fronts on Fig. 4.1f). The SHW/WSW front was south of the subsurface LSW/WSW front in all months except June. Surface temperatures of the SHW and WSW were seasonally variable, with the lowest and highest temperatures occurring in April and August, respectively (Table 4.2).

Table 4.2. Surface temperature range of fishing stations within the Shelf Water (SHW), Warm Slope Water (WSW) and Gulf Stream (GS) or Warm Core Rings (WCR) during the standard survey series.

Survey	SHW	WSW	WCR/GS
Dec (N112)	6.1-11.1	12.3-14.4	15.0-19.3
Feb (N096)	1.5-8.3	10.1-14.8	-
Apr (N119)	1.7-4.8	8.5-15.5	16.4-18.9
Jun (N122)	10.5-14.5	15.4-21.0	22.1-22.5
Aug (N126)	16.8-20.0	20.5-25.4	-
Oct (N110)	11.2-17.7	18.0-23.9	-

4.3 Results

4.3.1 Ordinations

For each survey, the eigenvalue of the first axis (depicted by the horizontal axes in Fig. 4.2) was always much larger than those of the other axes (Table 4.3), indicating that the gradient represented by the first axis was by far the most important. Surface and 200 m temperature, surface salinity and bottom depth were strongly correlated with the first axis (Table 4.3). Surface temperature followed by surface salinity was the best predictor of station position on the first axis in December, February and October (Table 4.3). Temperature at 200 m depth was a slightly better indicator in April, June and August than surface temperature and also than surface salinity in April and August. Bottom depth was generally a weaker predictor than the other variables. Temperature at 200 m in October (N110, Table 4.3) was the only physical variable to significantly correlate with the second axis.

Figure 4.2 shows the sites for each survey plotted by their ordination scores on the first and second DCA axes. Lines superimposed on the plots indicate the station groups determined by TWINSPAN. Station groups are numbered (from left to right) 2 and 3, or 1, 2 and 3, if two or three TWINSPAN groups were formed, respectively. Clearly, the first axis represents a gradient of decreasing water temperature, salinity and bottom depth. For each survey, stations placed at the right end of the horizontal axis were closest to the 1000 m contour and in the coldest water, stations on the left

Table 4.3 Eigenvalues of Axes 1 through 4 of Detrended Correspondence Analyses (DCA) by cruise and Pearson correlation coefficients between station scores and water column depth, surface temperature, surface salinity and temperature at 200 m (* - significance at 5% probability).

Cruise	Variable	Axis1	Axis2	Axis3	Axis4
December (N112)	Eigenvalue	0.250	0.068	0.049	0.029
	Depth (m)	-0.73*	-0.07		
	Sur-temp	-0.92*	0.17		
	Sur-salin	-0.90*	0.17		
	200m-temp	-0.82*	-0.26		
February (N096)	Eigenvalue	0.292	0.070	0.036	0.023
	Depth (m)	-0.74*	-0.21		
	Sur-temp	-0.93*	-0.07		
	Sur-salin	-0.88*	-0.03		
	200m temp	0.75*	-0.27		
April (N119)	Eigenvalue	0.213	0.078	0.006	0.001
	Depth (m)	-0.86*	0.20		
	Sur-temp	-0.83*	0.14		
	sur salin	-0.86*	-0.05		
	200m-temp	-0.90*	-0.38		
June (N122)	Eigenvalue	0.454	0.099	0.051	0.017
	Depth (m)	-0.85*	0.07		
	Sur temp	-0.94*	-0.12		
	sur-salin	-0.98*	-0.07		
	200m-temp	-0.97*	-0.11		
August (N126)	Eigenvalue	0.217	0.059	0.038	0.011
	Depth (m)	-0.80*	-0.05		
	Sur-temp	-0.90*	-0.16		
	sur-salin	-0.91*	0.28		
	200m-temp	-0.93*	0.10		
October (N110)	Eigenvalue	0.331	0.079	0.053	0.037
	Depth (m)	-0.82*	0.20		
	Sur temp	-0.88*	0.10		
	sur-salin	-0.87*	0.16		
	200m-temp	-0.81*	0.36*		

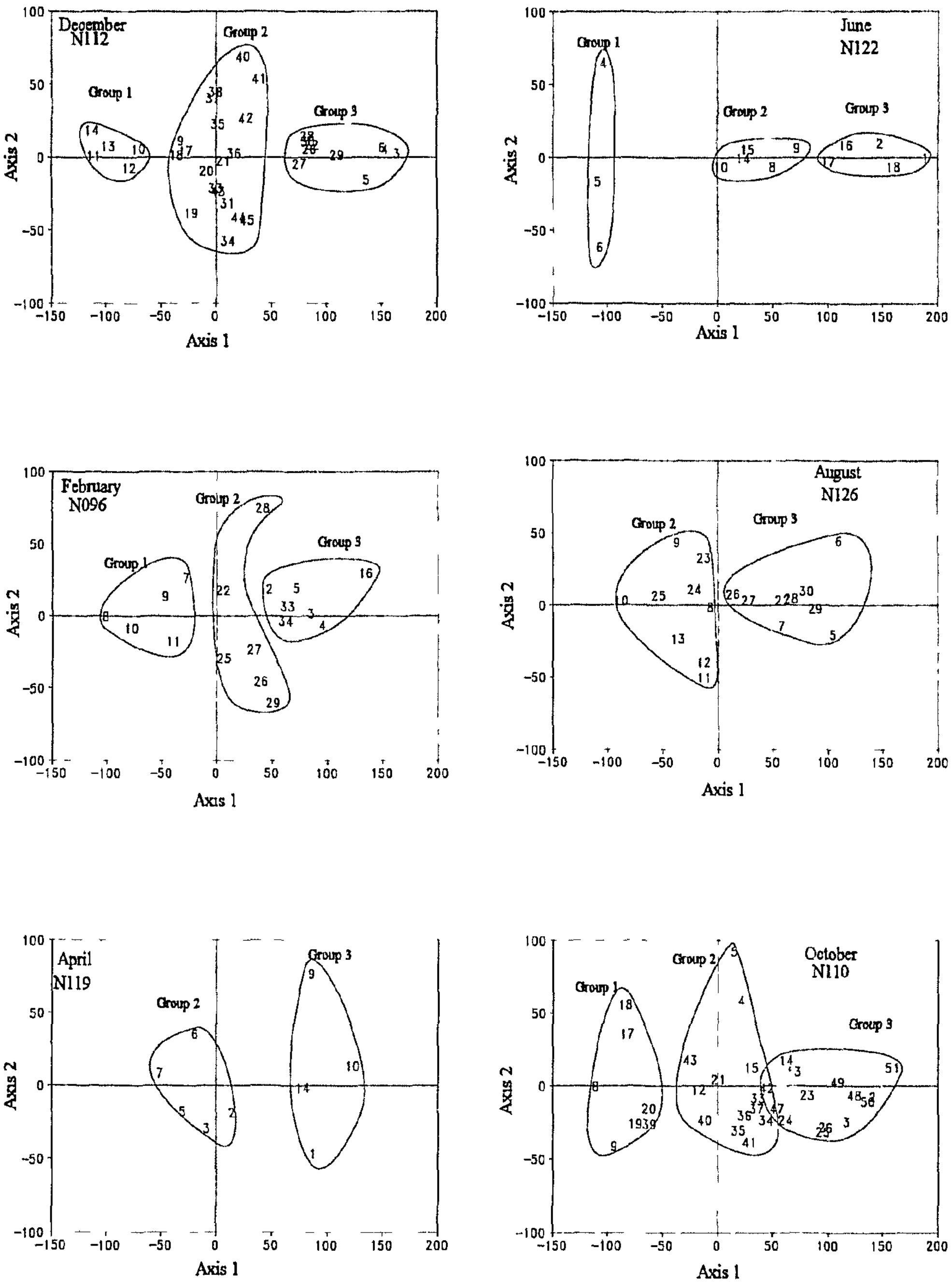


Figure 4.2. Plots of station scores on the first two axes of the detrended correspondence analyses. Lines enclosing groups of stations indicate the corresponding TWINSPAN groups.

were the furthest seaward and in WCR or WSW.

Causes of the gradients represented by the second axes (vertical axis) are unclear. Trial runs indicated that relative station position on axis 2 was strongly affected by the choice of transformation. Stations widely dispersed on the second axis, such as Group 2 of the December ordination (Fig. 4.2a) were much closer together when no data transformation was employed. This may have occurred because DCA always separated stations along the first axis based upon the relative abundance of the dominant species. Infrequent species had little effect on the ordination unless a strong data transformation was used, after which DCA used the second axis to exhibit trends in their relative abundance. For example, in the ordination of the December survey, station 40 is separated from stations 34 and 36 on the second axis, but there is no corresponding gradient in the relative abundances of the most abundant species which were *Lobianchia dofleini, Ceratoscopelus maderensis,* and *Benthosema glaciale* . Plotting the species scores showed that the gradient was reflecting the relative numbers of species with low overall abundance such as *Bolinichthyes indicus, Diaphus metopoclampus,* and *Lobianchia gemellarii.*

First axes lengths varied from 1.8. s.d. (April) to 3.0. s.d. (June, Fig. 4.2), indicating a low degree of separation between stations, with all stations within each cruise having some species in common. Discontinuities in the spread of stations across axis 1 suggest some abruptness in the rate of species change between stations in four cruises. A gap of 0.4 s.d. separates Group 2 from

Group 3 in December, and Group 1 from 2 in October (Fig. 4.2). Larger intervals of 0.7 and 1.1, respectively, separate Group 2 from 3 in April and Group 1 from 2 in June (Fig. 4.2). In contrast, the TWINSPAN groups are not obvious in the ordinations of the February and August cruises as the stations are dispersed evenly across the first DCA axis. The divisions between groups in other cruises, such as between Groups 2 and 3 in June and October (Fig. 4.2) are also very slight, being equal or less than the distance between stations within the group. These indicate that, for most of the surveys, differences between station groups are not apparent in ordination.

4.3.2 Classification

TWINSPAN and PSi classifications are discussed for each of the cruises individually. TWINSPAN groups are displayed in Figure 4.2 as they appear in a two dimensional DCA ordination. Figure 4.3 shows the two-way tables of species and stations produced by TWINSPAN for each survey. Only species which contributed greater than 0.1% to the total cruise catch are displayed. The sixth abundance level (>500 individuals) was not shown to increase contrast between the shades of the other five abundance levels. Site classification by PSi is shown as a dendrogram in the upper right corner of Figure 4.3. Catch statistics for the TWINSPAN grou are summarized in Table 4.4.

December (N112)

TWINSPAN divided the stations into three groups (Figs. 4.2a, 4.3a). Percent similarity only differed from TWINSPAN by including station 17 in Group 1 rather than Group 2 (Fig. 4.3a). Hydrographic characteristics of the stations within TWINSPAN Groups 1, 2 and 3 generally corresponded with WCR, WSW and LSW water masses, respectively, but stations adjacent to the subsurface fronts sometimes grouped with sites on the opposite side. Stations 9 and 10 were sampled near the edge of the WCR but their species composition was similar to the stations of Group 2 and 1, respectively. Group 2 also contained three stations (40, 41, 42) with transitional LSW characteristics (Halliday et al. 1995), in addition to most of the WSW stations and station 9. Two WSW stations (29 and 30) sampled near the front joined with the LSW stations of Group 3. The cold surface SHW was considered as a possible modifier of species composition which caused two adjacent WSW stations (30 and 31) to join with station groups 3 and 2, respectively. Stations 30 and 31 were sampled on landward and seaward sides, respectively, of this surface front and the most abundant species were *B. glaciale* (27 %, 18 other species) and *C. maderensis* (83%, 27 species), respectively. However, at other stations situated on either side of the front (e.g. 19 and 20, 33 and 34), *C. maderensis* was always dominant and the stations did not separate during classification, all being in Group 2.

Faunal characteristics shared by a site group demonstrate that

Figure 4.3. Two-way station-by-species tables produced by TWINSPAN with the stations shown in groups. Degree of shading indicates the level of abundance (numbers) of a species at that station. Symbols above station number indicate water mass designation (WCR - Warm Core Ring, WSW - Warm Slope Water, LSW - Labrador Slope Water). Dendrogram shows results of classification by Percent Similarity index.

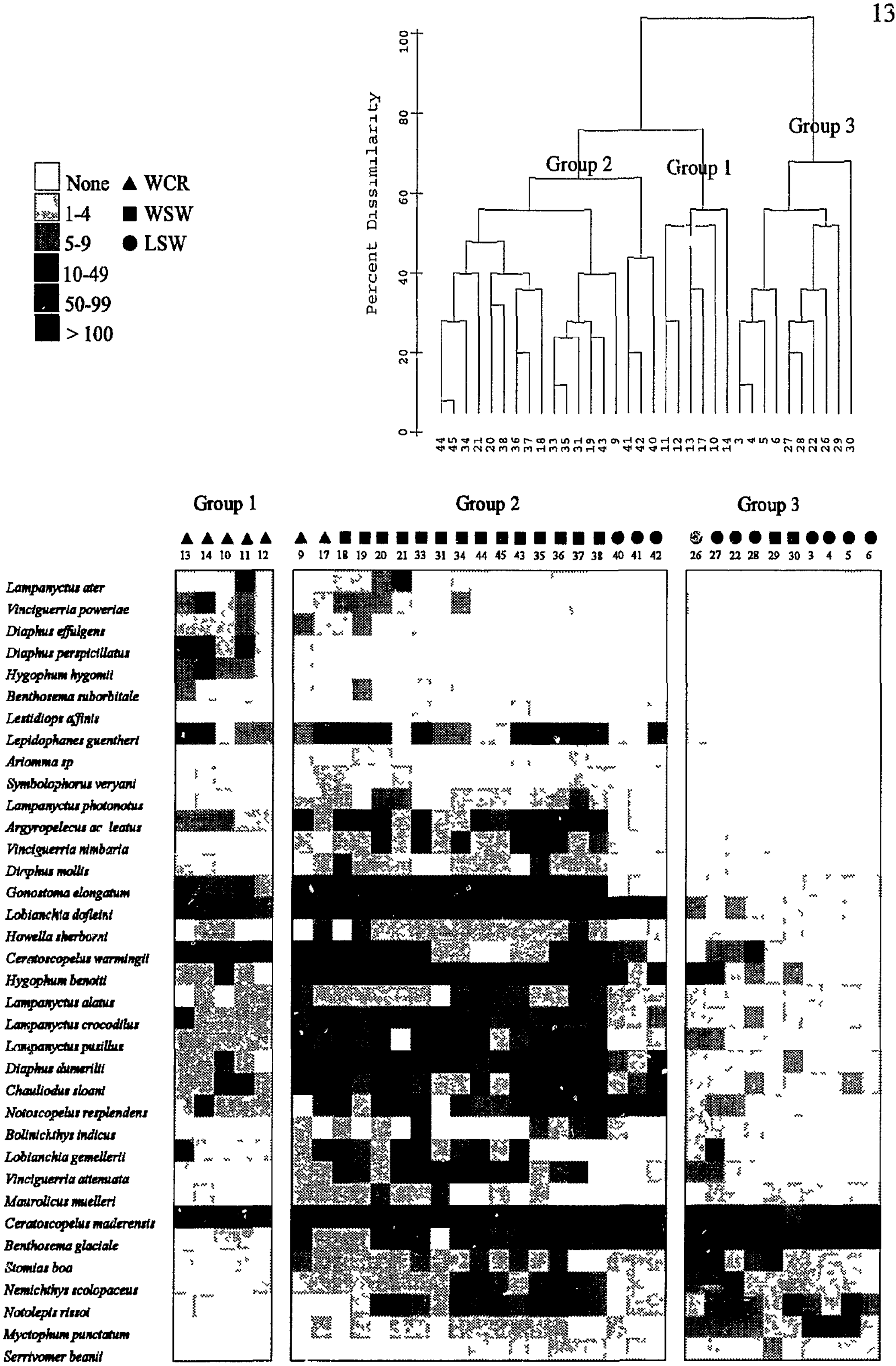


Figure 4 3a December (N112).

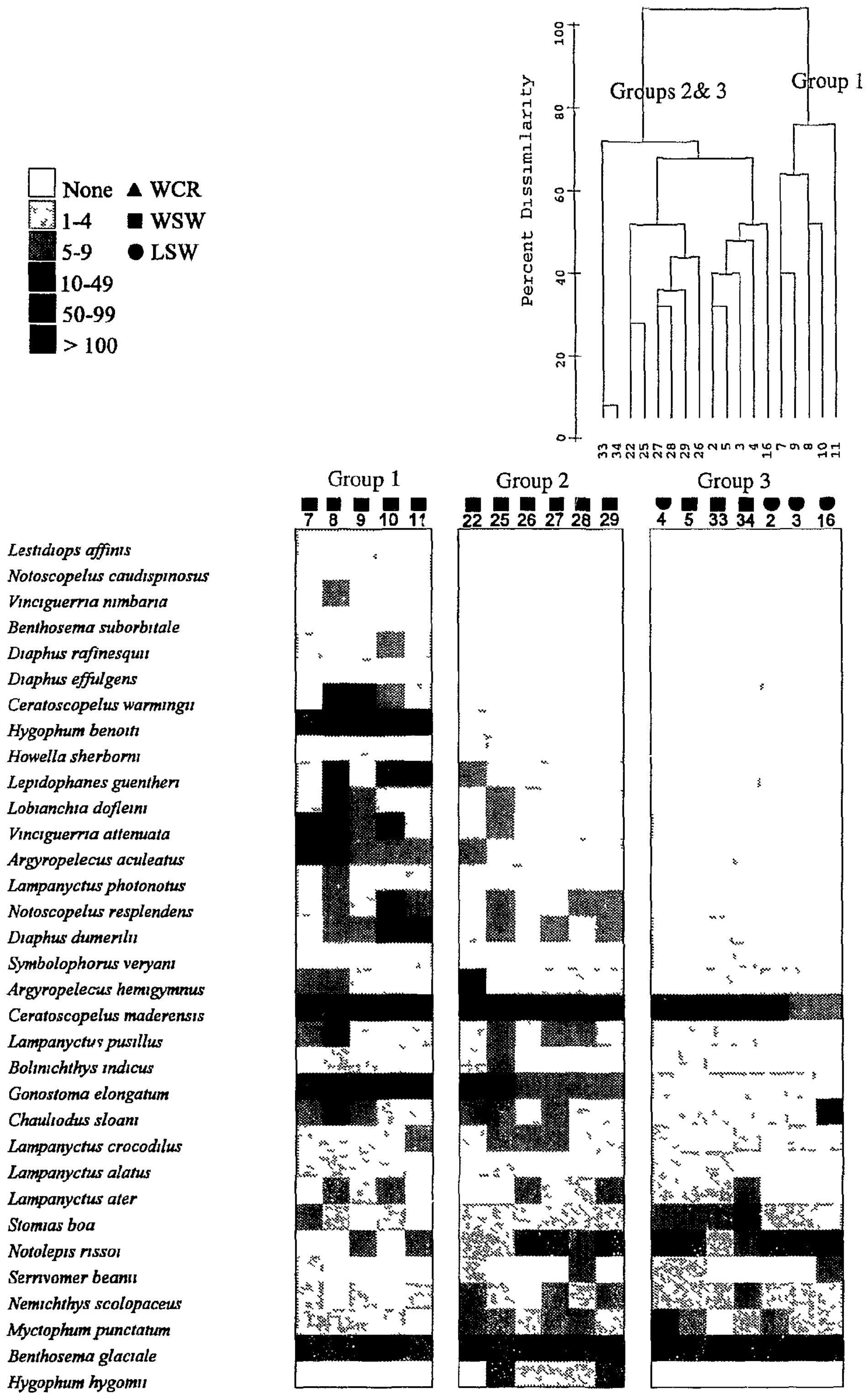


Figure 4 3b February (N096)

Figure 4.3c. April (N119).

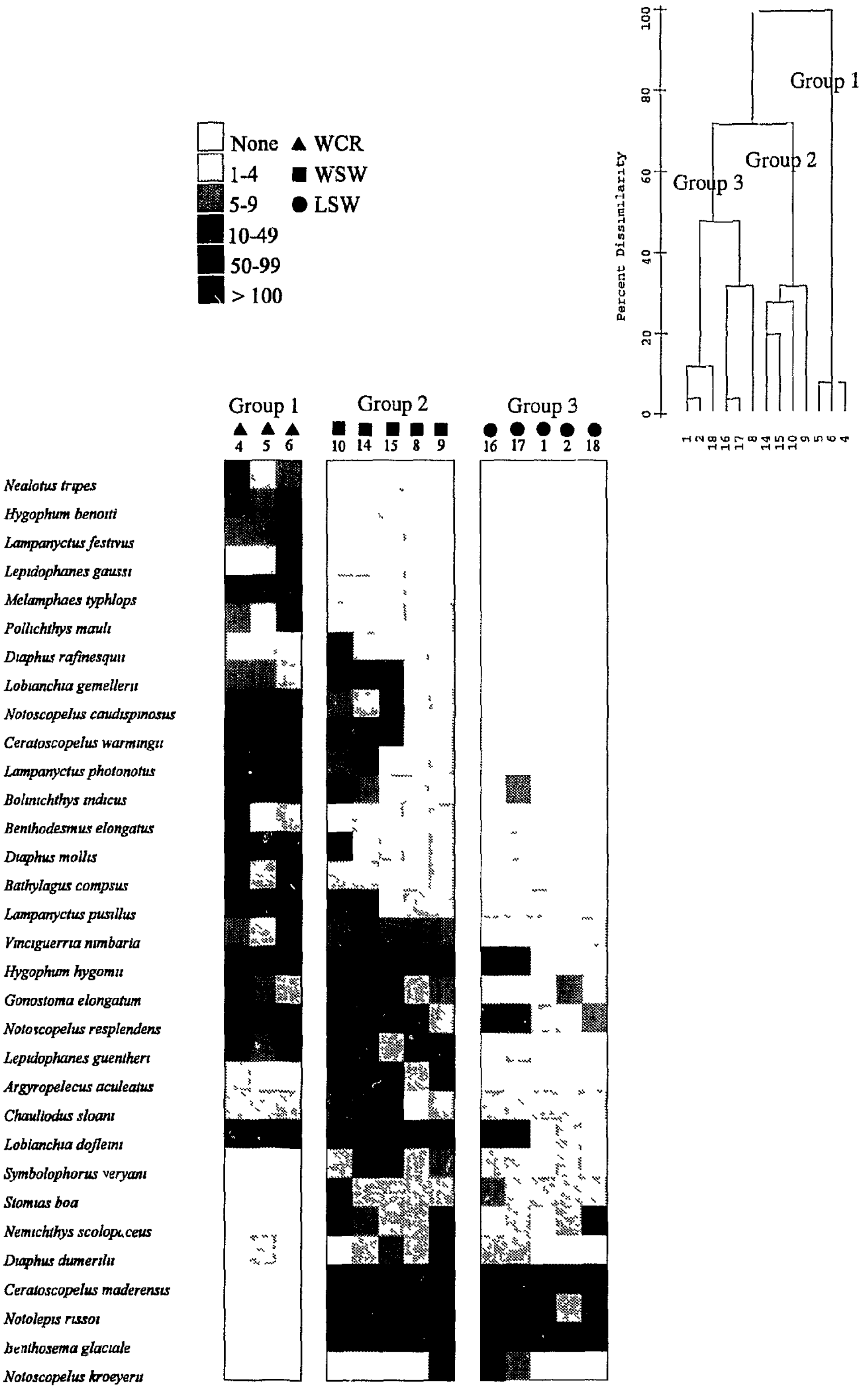


Figure 4.3d. June (N122)

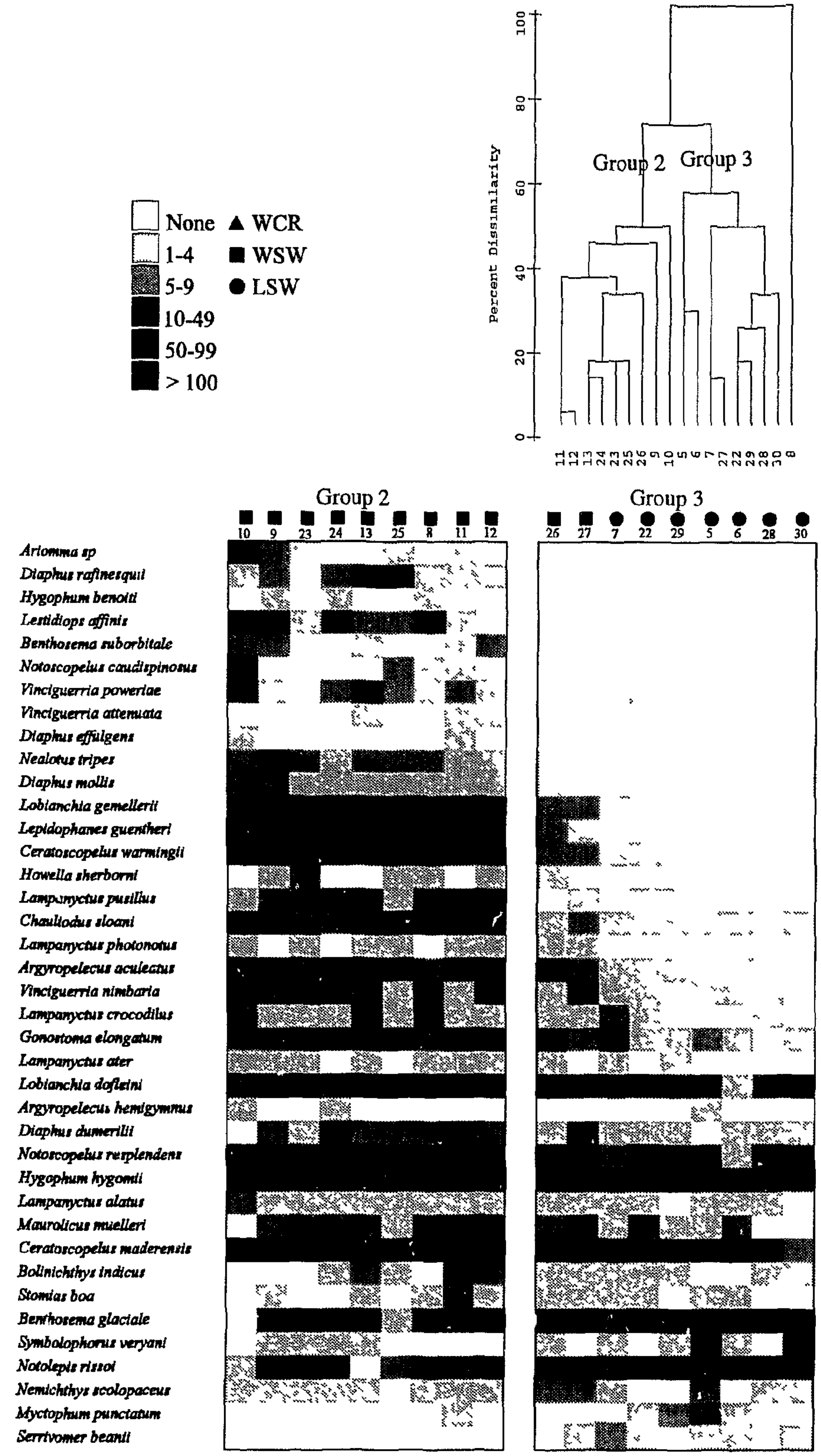


Figure 4 3e. August (N126)

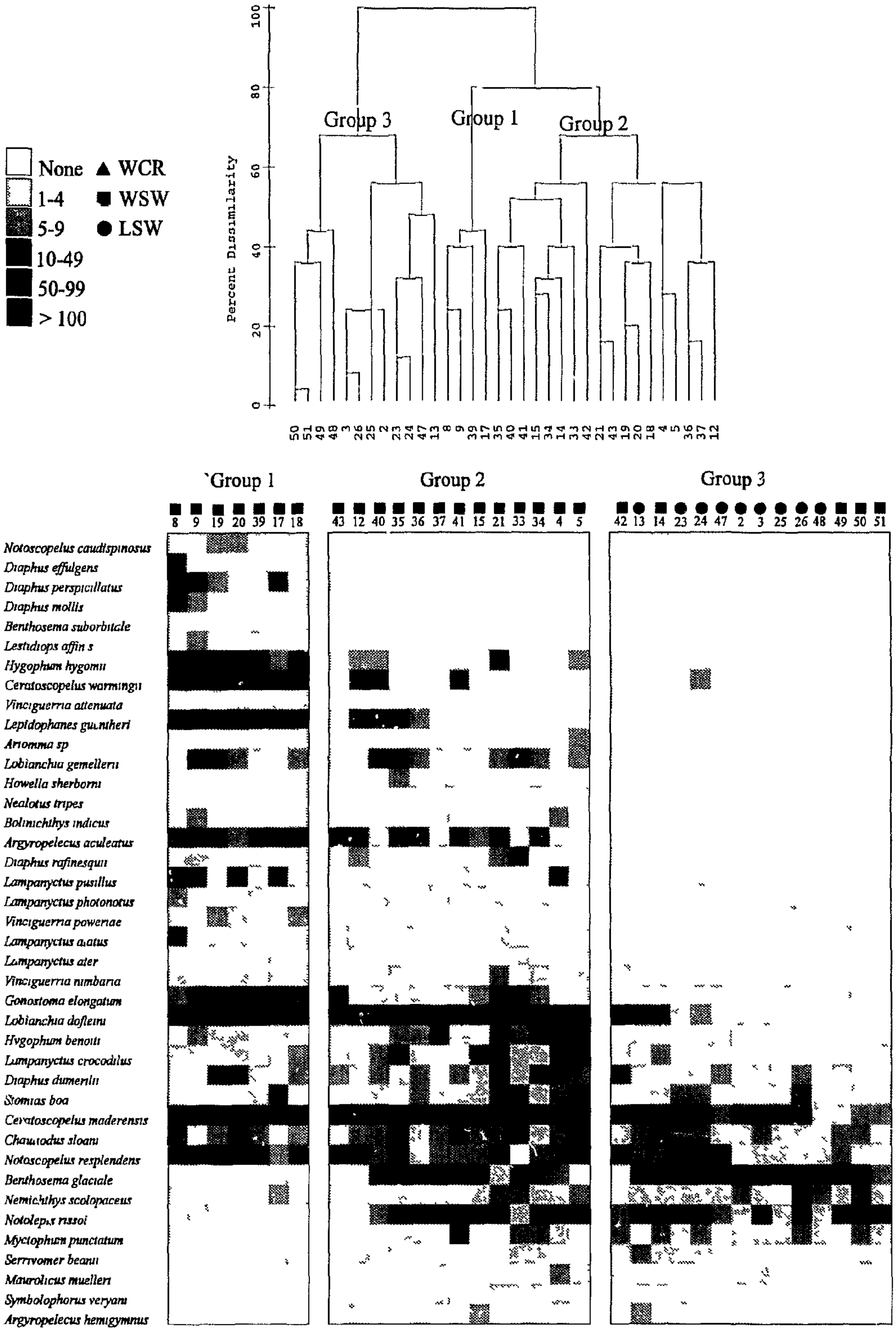


Figure 4 3f October (N110)

TWINSPAN uses both relative abundance and species richness to classify sites. Groups 1 and 2 shared a number of abundant and common species (Fig. 4.3a). *C. maderensis* and *L. dofleini* were abundant in both groups, but relatively more abundant in Group 2 (Table 4.4). Species evenness was higher in Group 1 where five species contributed more than 5% to the total catch, compared to two species in Group 2 (Table 4.4). I interpreted WCR stations 9 and 17 as misclassified to Group 2 due to their transitional species composition. Species richness was high at both stations but *C. maderensis* occurred at station 9 in numbers 5-10 times higher than at any of the Group 1 sites while two distinctive Group 1 species (*D. perspicillatus, Hygophum hygomii*) were missing from station 17. Stations 40-42 were also transitional as they were similar to Group 3 stations in being dominated by *B. glaciale* but differed in having a higher species richness (23-25 species) than most of the Group 3 sites, although still less than the other Group 2 sites.

The Group 3 sites can be characterized by the absence of many species common to the other two station groups. All the species captured at the Group 3 sites also occurred in Group 2, and most appeared in at least some of the Group 1 stations (Fig. 4.3a). Group 3 was dominated by *B. glaciale,* a frequently and rarely occurring species in Groups 2 and 1, respectively (Fig. 4.3a, Table 4.4). *Lobianchia dofleini* occurred in low numbers at only 50% of the Group 3 stations while *C. maderensis* decreased from 68% of the catch in Group 2 to 9% in Group 3. Evenness was slightly lower in Group 3 than Group 2

Table 4.4. Characteristics of station groups determined by Twinspan. (no. unique) - species unique to that station group; No. species > 1% - species whose proportion exceeded 1 % of the pooled station catch, ()-combined % total catch of those species; abundant species comprised ≥ 5% of catch.

Group characteristics	Station Group 1	Station Group 2	Station Group 3
December: N112			
No. sets	5	19	10
No.species (no. unique)	67 (6)	114 (42)	45 (2)
No. individuals	1532	38640	4011
No. species > 1%	16 (86.1)	9 (92.5)	6 (91.8)
Abundant species (%)	*Ceratoscopelus maderensis* (31.6)	*Ceratoscopelus maderensis* (68.1)	*Benthosema glaciale* (74.6)
	Lobianchia dofleini (11.2)	*Lobianchia dofleini* (12.6)	*Ceratoscopelus maderensis (9.1)*
	Ceratoscopelus warmingii (10.6)		
	Diaphus perspicillatus (7.8)		
	Lepidophanes guentheri (5.9)		
February: N096			
No. sets	5	6	7
No. species (no. unique)	71 (28)	57 (13)	36 (7)
No. individuals	7012	2093	3069
No. species > 1%	5 (91.4)	13 (90.4)	5 (94.5)
Abundant species (%)	*Ceratoscopelus maderensis* (72.4)	*Benthosema glaciale* (61.7)	*Benthosema glaciale (86.1)*
	Hygophum benoiti (10.1)	*Ceratoscopelus maderensis* (10.3)	
	Benthosema glaciale (6.5)		
April: N119			
No. sets		5	4
No. species (no. unique)		66 (39)	29 (2)
No. individuals		5810	6884
No. species > 1%		7 (89.7)	2 (97.3)
Abundant species (%)		*Benthosema glaciale* (49.9)	*Benthosema* glaciale *(95.3)*
		Ceratoscopelus maderensis (24.7)	*Ceratoscopelus maderensis* (2.0)
		Hygophum hygomii (7.2)	
June: N122			
No. sets	3	5	5
No. species (no. unique)	69 (19)	79 (17)	38 (8)
No. species > 1%	16 (87.6)	12 (91.7)	4 (97.1)

Table 4.4 cont.

	Station Group 1	Station group 2	Station group 3
No. individuals	2776	6687	4901
Abundant species (%)	*Diaphus mollis* (14.5)	*Hygophum hygomii* (26.3)	*Benthosema glaciale* (79.9)
(June cont.)	*Hygophum hygomii* (10.6)	*Lobianchia dofleini* (16.1)	*Notolepis rissoi* (8.8)
	Notoscopelus resplendens (9.7)	*Ceratoscopelus maderensis* (16.0)	*Ceratoscopelus maderensis* (6.3)
	Bolinichthys indicus (9.6)	*Notolepis rissoi* (8.8)	
	Lobianchia dofleini (8.1)	*Benthosema glaciale* (7.1)	
	Ceratoscopelus warmingii (5.7)		
	Hygophum benoiti (5.4)		
	Notoscopelus caudispinosus (5.4)		
	Lampanyctus photonotus (5.2)		
August: N126			
No. sets		9	9
No species (no. unique)		101 (55)	54 (8)
No. individuals		17294	6463
No. species > 1%		10 (91)	6 (84.8)
Abundant species (%)		*Lobianchia dofleini* (36.3)	*Benthosema glaciale* (53.0)
		Hygophum hygomii (18.2)	*Notoscopelus resplendens* (8.4)
		Ceratoscopelus maderensis (12.9)	*Lobianchia dofleini* (8.1)
		Notoscopelus resplendens (9.4)	*Hygophum hygomii* (7.6)
			Notolepis rissoi (6.5)
October: N110			
No. sets	7	13	14
No. species (no. unique)	93 (29)	79 (13)	53 (5)
No. individ.	6175	7650	2492
No. species >1%	12 (91.6)	14 (93.3)	10 (92.1)
Abundant species (%)	*Ceratoscopelus maderensis* (38.6)	*Ceratoscopelus maderensis* (49.4)	*Benthosema glaciale* (40)
	Lobianchia dofleini (18.5)	*Lobianchia dofleini* (21.0)	*Ceratoscopelus maderensis* (20.6)
	Notoscopelus resplendens (9.1)		*Notolepis rissoi* (8.0)
			Lobianchia dolfleini (7.1)
			Notoscopelus resplendens (5.5)

(Table 4.4), however, the stations in both groups show a pattern of a few very abundant (> 100 individuals) species and several medium abundance species (10-50 individuals).

February (N096)

TWINSPAN separated the Stations at the southern end of the easternmost transect (stations 7-11) into Group 1, and roughly separated the mid-slope and near shelf edge stations into Groups 2 and 3, respectively. Only two station groups were formed by PSi; one was identical in station composition to TWINSPAN's Group 1, the other combined TWINSPAN's Group 2 and 3 (Fig. 4.3b). Station 11 was quite dissimilar to the other Group 1 stations due to a total catch about four times larger than at any other station, of which 93% were *C. maderensis*. TWINSPAN Group 1 and 2 were WSW stations, Group 3 was comprised of LSW stations and three (5, 33 and 34) WSW sites, the latter two of which were in a pocket of WSW separated from the main body of WSW. Surface water conditions are associated with the differences in species composition between Groups 1 and 2, since the cold SHW lying over the Group 2 stations was 75-120 m thick.

Abundant species overlapped among the three TWINSPAN Groups (Table 4.4), but species richness, and relative abundance differed. Group 1 was dominated by *C. maderensis* and *Hygophum benoiti*, Group 2 and 3 by *B. glaciale*. Lack of evenness of Group 1 (which makes it similar in this characteristic to

Group 2), and the large contribution by *C. maderensis* to the total catch of Group 1 are because station 11 contributed 50% of all individuals in that group. Removing station 11 shifted the percent abundance of *C. maderensis* and *H. benoiti* to 44.8% and 18.1%, respectively, and increased the number of species contributing more than 1% of the total catch from 5 to 11. TWINSPAN may not have separated station 11 from stations 7 through 10 because the pseudospecies levels were not set high enough to differentiate it. However, stations 7 through 11 differ from all other stations by having high numbers of both *C. maderensis* and *H. benoiti.*

Reasons for the separation of Groups 2 and 3 by TWINSPAN are unclear as both groups were similar in species composition (Fig. 4.3b). *Benthosema glaciale* accounted for a large proportion of the catch of the stations comprising Group 2 (44-85%) and Group 3 (41-95%), and the second ranked species accounted for < 20% of the catch in all samples. Number of species per tow ranged from 25-29 in Group 2 and 14-21 in Group 3. The WSW stations 5, 33 and 34 were joined with the LSW sites in Group 3 because they had low species richness (15-16 species), and because stations 33 and 34 were dominated by *B. glaciale* (95% total catch). In conclusion, PSi was more effective than TWINSPAN in classifying this survey. WSW stations could be differentiated into those at which *C. maderensis* and *H. benoiti* were abundant, or at which *B. glaciale* were dominant. The latter group of stations had similar faunal characteristics to the LSW stations.

April (N119)

TWINSPAN and PSi divided the few stations sampled in April into identical groups (Fig. 4.3c). Group 2 contained the southeastern WSW sites while Group 3 was comprised of the two LSW sites and WSW sites 1 and 14. Both TWINSPAN groups were dominated by *B. glaciale,* but a number of species occurring in Group 2 were absent in Group 3. Seven species contributed more than 1% to the total catch of Group 2 compared to two species in the Group 3 stations (Table 4.4). Although stations 1 and 2 were both covered by SHW, differences in its thickness and temperature may have caused the lower number of species captured at station 1. The SHW was a 75 m deep layer at station 1 with a temperature of 1 °C in the upper 50 m, compared to a layer a few metres thick at station 2. Station 14 was an outlier. Few animals were taken, of which 51% were *B. glaciale.*

June (N122)

TWINSPAN separated WCR stations 4-6 into Group 1, WSW into Group 2 and LSW into Group 3 (Figs. 4.2d, 4.3d). The PSi classified the stations similarly except that station 8 was placed in Group 3. Stations were classified by PSi solely by dominant species identity while disregarding percent abundance or species richness. Station 8 was similar to the Group 3 stations in the high relative abundance of *B. glaciale.* However, the catch contained 37 species (compared to 10-23 in other Group 3 stations), of which *B. glaciale* comprised 30% (51%-94% in the Group 3 stations).

The water mass characteristics of the three TWINSPAN groups are homogenous. Group 1 sites were all within the WCR present on the easternmost transect, Group 2 sites in the centrally located WSW and Group 3 in the LSW present on the shoreward ends of the eastern and western transects (Fig. 4.1d).

Species with the highest relative abundance differed between station groups, but at least one of the top three species was shared between adjacent groups. An obvious decrease occurred in species richness and evenness from Groups 1 to 3 (Table 4.4). Several species were abundant within the Group 1 stations or in Groups 2 and 3, but not both (Fig. 4.3d). *Notolepis tripes, H. hygomii, Diaphus mollis* and *Melamphaes typhlops* were nearly exclusive to the WCR sites and station 10 outside the ring, at best being encountered in low numbers at other stations. This ring was younger than the one encountered in December since species with temperate or subpolar origins (e.g. *C. maderensis, B. glaciale*) were not captured at stations within the ring.

When the rows of the two-way table (Fig. 4.3d) are viewed from left to right, the station order displays decreasing abundance of species such as *Ceratoscopelus warmingii, C. maderensis* and *L. dofleini,* and increasing abundance of *B. glaciale.* The stations are not ordered along a gradient as was noted in the December survey (Figs. 4.2a, 4.3a) when stations sampled nearer the shelf edge were also further right in the two way table. Still, in each station group there are a few 'transitional' stations. These have a species composition similar to the station group occurring to the left, such as station 10 with Group 1, and stations 16 and 17, which seem more like group 2 stations than the geographically adjacent station 18 (Fig. 4.3d).

August (N126)

The first TWINSPAN division created two equally sized groups. Further divisions resulted in station groups which could not be discriminated in the DCA ordination. Classification by PSi was similar except that station 26 joined Group 2 and station 8 was an outlier. TWINSPAN Group 2 was composed of WSW stations while Group 3 contained the LSW stations and WSW stations 26 and 27 (Fig. 4.1e).

Differences between the two station groups were not determined by the most abundant species since three of the top four species in Group 2 were also dominant in Group 3 (Table 4.4). Species richness and evenness were higher in Group 2, and the relative abundance of *B. glaciale* was lower than in Group 3 (Table 4.4). Species whose distributions corresponded to the TWINSPAN divisions were either generally low in abundance (e.g. *Diaphus rafinesquii, Nealotus tripes*) or predominantly tropical and semi-subtropical in origin (e.g. *C. warmingii, Lepidophanes guentheri*, Fig. 4.3e). TWINSPAN included stations 26 and 27 with the colder water sets due to their low numbers of *N. tripes* and *L.*

gemellarii relative to the Group 2 sites. Looking across the rows from left to right, very abundant species showed patterns of gradually decreasing abundance (*Argyropelecus aculeatus, L. dofleini*), no overall difference in abundance (*Notoscopelus resplendens, H. hygomii, C. maderensis*) or gradual increase in abundance (*B. glaciale, N. rissoi*). The PSi divisions can be easily interpreted on the basis of the identity of the top-ranking species: *H. hygomii* ranks first or second in the lefthand group, *B. glaciale* ranks first or second in the righthand group and the outlier, station 8, is the only station dominated by *N. resplendens* (Fig. 4.3e).

October (N110)

TWINSPAN formed three station groups (Fig. 4.3f). The PSi shifted three stations from TWINSPAN Group 1 (stations 18, 19 and 20) and two from Group 3 (14, 42) into Group 2. TWINSPAN Groups 1 and 2 were WSW stations, Group 3 was composed of the LSW sites and five WSW stations (14, 42, 49, 50, 51). All of the Group 2 stations, although in WSW according to 200 m temperatures, were landward of the SHW/WSW surface front. It is unlikely that the SHW would have much effect on species composition since surface SHW water temperatures were as warm as those of the WSW in the late winter or early spring (Table 4.2). However, Group 2 sites were classed as WSW but most showed evidence of extensive mixing occurring between layers of LSW and WSW (Halliday et al. 1995).

Station groups were homogenous (Table 4.4); species evenness was similar due to a higher evenness in Group 3 than seen in the other cruises, and the three top ranked species of Group 1 were also among the most abundant species of Groups 2 and 3. Group 1 can be defined by its species composition (Fig. 4.3f) as some of its relatively abundant species (*D. perspicillatus* and *D. mollis*) were seldom captured at other sites. Groups 2 and 3 differed in the relative abundances of their shared species, *L. dofleini* and *C. maderensis* were more abundant in Group 2 while *B. glaciale* and *N. rissoi* were more abundant in Group 3. Group 3 stations also had fewer species than the other two groups.

The three station groups formed by PSi are, in general, stations at which *C. maderensis* and *L. dofleini* were the most abundant species but contributed < 50% and > 50% of the total sample (Group 1 and 2, respectively), or the most abundant species were *B. glaciale* or *N. rissoi* (Group 3). Stations 18 through 20 were classified as Group 2 because of a high relative abundance (60-69%) of *C. maderensis* and *L. dofleini.* Stations 14 and 42 were joined with the Group 2 sites because *L. dofleini* contributed 26% and 36% of the total catch, respectively.

In conclusion, the three station groups were generally consistent in their relative geographic position and hydrographic characteristics. Stations were clustered into two groups in April and August, and three in the other four surveys. Group 1 was composed of the WCR stations sampled in December and June, and the WSW stations located furthest seaward with the warmest surface temperatures in February, and least degree of mixing with the LSW in October.

4.3.3 Comparison of temporal patterns among station groups

Figure 4.4 displays the retransformed geometric mean numbers of individuals per tow, average number of species per tow, and species evenness (also summarized in Table 4.4) of the sixteen TWINSPAN groups identified in total in the six cruises.

In four cruises, catches were higher in Group 2 than the other station groups (Fig. 4.4a). Group 1 catches only exceeded Group 2 in the February and October cruises when the stations were all from WSW. Seasonal trends are not apparent in Group 2 catches, possibly because of the shifts in abundance of the dominant species, from *C. maderensis* in December, *B. glaciale* in February, to *H. hygomii* and *L. dofleini* in June and August. In Group 3, low catches during the fall and winter cruises and the threefold increase in abundance in April are related to variation in the abundance of *B. glaciale*. Group 3 abundance in spring and summer was much higher than in autumn and winter, indicating strong seasonal variation in abundance. Figure 4.4b shows a seasonal progression of increasing species richness (as number of species per tow) from February to August in Group 2, and April to August in Group 3, followed by declining richness between October and February.

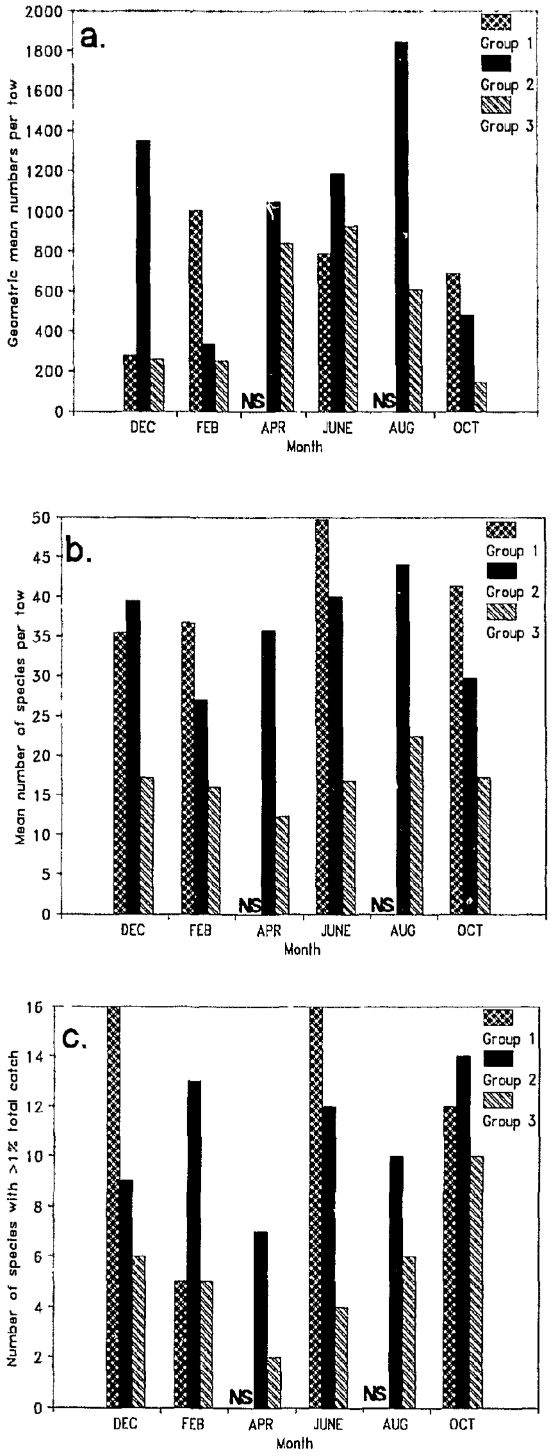


Figure 4.4. Comparisons among TWINSPAN groups of a) geometric mean catch (numbers fish per tow); b) mean numbers of species per tow; c) evenness (numbers of species contributing > 1% to total catch). NS - no samples.

Evenness was highest in Group 1 in December and June when only ring sets were sampled (Fig. 4.4c). Group 2 sets displayed variable evenness from a low of 7 species exceeding 1% of total catch in April to a high of 14 in October. Evenness in Group 3 sets was inversely related to the abundance of *B. glaciale,* increasing from 2 species in April to 10 in October (Table 4.4, Fig. 4.4c).

4.3.4 Comparison of temporal patterns of abundant species

A species was considered abundant if it contributed greater than 5% of the total catch of that TWINSPAN group. Variations in catch for the 13 resulting species are displayed in Figure 4.5 as geometric mean numbers of individuals per tow in each TWINSPAN group and referred to in the text as individuals per tow, retransformed to the arithmetic scale. The zoogeographic distribution pattern classification of the abundant myctophid species is taken from Backus et al. (1977).

Diaphus perspicillatus, N. caudispinosus, D. mollis and *B. indicus* were restricted in their distribution. They were always associated with WCR sets and occurred in low abundance in Group 2 sets and rarely in Group 3 sets. *Diaphus perspicillatus* is a tropical (i.e. Caribbean) species rare in the Sargasso Sea near Bermuda (Karnella 1987). It was only abundant in the fall/winter cruises, reaching a peak abundance of 14 individuals per tow in December (Fig. 4.5). *Notoscopelus caudispinosus, D. mollis,* and *B. indicus* were most abundant in June WCR sets, occurring at densities of 41, 123, and 67

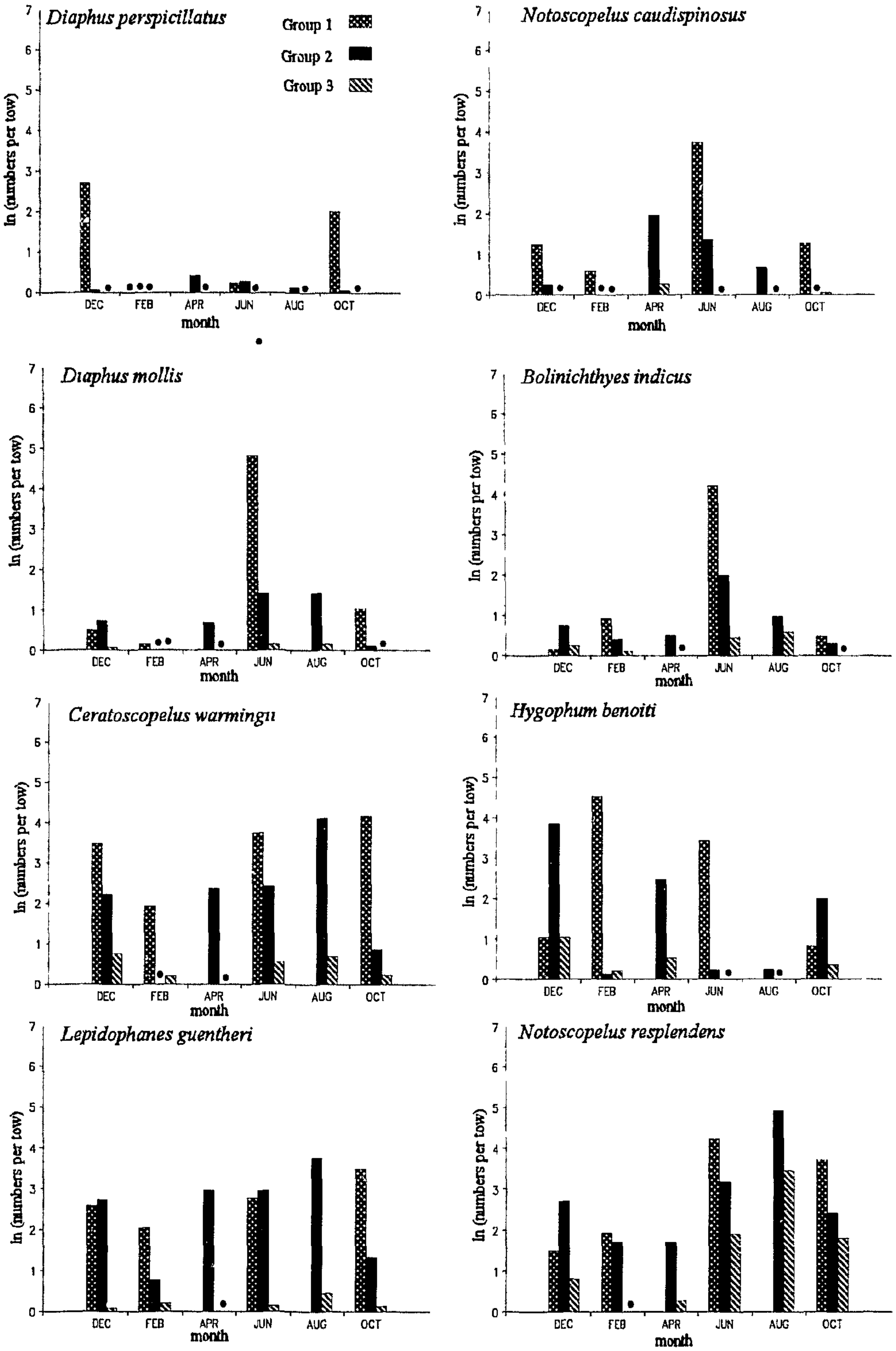


Figure 4.5. Mean abundance (ln numbers per tow) of the 13 most abundant species among TWINSPAN groups and surveys. ● - none caught.

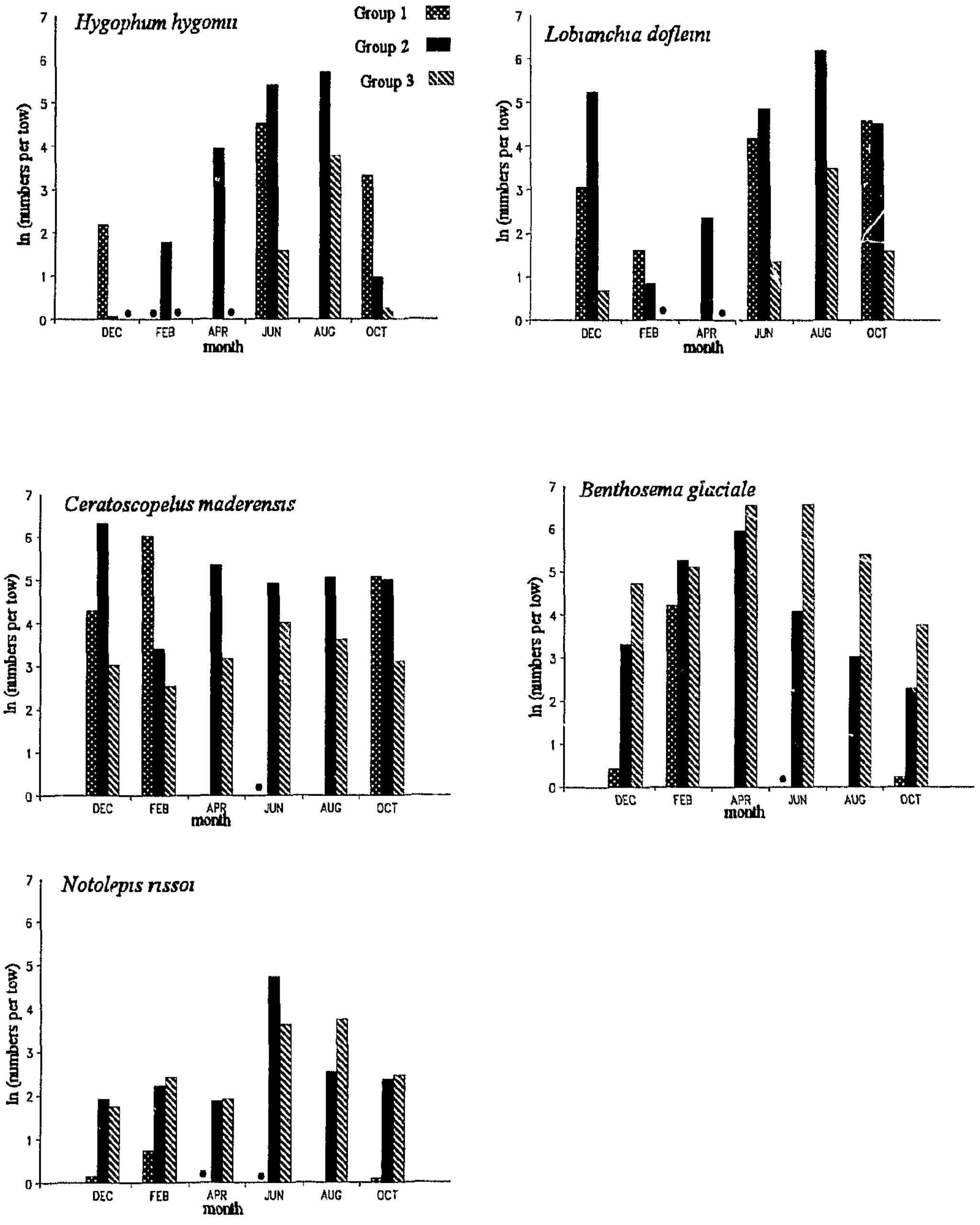


Figure 4.5 cont.

individuals per tow, respectively. All three of these species have distributions which include the Sargasso Sea, where they are common to very abundant (Gibbs et al. 1971; Karnella 1987; Gartner et al. 1989).

Ceratoscopelus warmingii, L. guentheri and *H. benoiti* were classified as abundant based on their numbers at Group 1 stations but were occasionally abundant in Group 2, though never among the most abundant species of these stations. Although *C. warmingii* only contributed more than 5% to the catch of Group 1 in June, the largest catches occurred in the Group 2 sets of August (60 ind/tow) and Group 1 sets of October (64 ind/tow). *Lepidophanes guentheri* was most abundant in Group 2 in August (42 ind/tow). *Ceratoscopelus warmingii* and *L. guentheri,* with tropical-subtropical and tropical distributions, respectively, are the first and third ranked myctophids of the Gulf of Mexico (Gartner et al. 1987). Highest densities of *H. benoiti,* a temperate-semisubtropical species, occurred in Group 1 in February (90 ind/tow). In December, it was more abundant in Group 2 (45 ind/tow) than Group 1 (2 ind/tow). In June, most *H. benoiti* were collected in Group 1 stations, with a single capture of 2 individuals in Group 2. Two were also captured in August in Group 2. Again, the occurrence of these three species was rare at Group 3 stations.

Highest densities of *N. resplendens* (tropical-subtropical distribution), *H. hygomii* and *L. dofleini* (both temperate-semisubtropical species) occurred in the Group 2 stations of August at 136, 300 and 483 ind/tow, respectively. These species were also abundant, but to a lesser degree, in the Group 3 stations of August. *Lobianchia dofleini* and *N. resplendens* occurred in Groups 1 and 2 of all cruises whereas *H. hygomii* was absent from Group 1 in February and very scarce in Group 2 in December. *Lobianchia dofleini* was missing from Group 3 in February and April; *N. resplendens* was absent in Group 3 in February and only two animals were caught at the four stations of Group 3 in April; and *H. hygomii* was absent from Group 3 from December to April. Strong seasonality was evident for all three species.

Ceratoscopelus maderensis (reclassified from temperate-semisubtropical to temperate by Backus and Craddock 1982) was present in every TWINSPAN group except Group 1 of June. Its highest abundance occurred in December in Group 2 (561 ind/tow), followed by Group 1 in February (414 ind/tow). The two cruises in which it was more abundant in Group 1 than Group 2 were also when Group 1 was a heterogenous collection of WCR and WSW stations. *Ceratoscopelus maderensis* was always more abundant in Group 2 than Group 3. No seasonal variation occurred in Groups 1 and 2 but there was some suggestion of it in Group 3.

Benthosema glaciale (subpolar-temperate distribution) was the only species consistently more abundant in Group 3 than other groups. Its highest densities occurred in April and June, at 695 and 702 ind/tow, respectively. It was most abundant in Group 2 in April at 386 ind/tow. In both groups, *B. glaciale* exhibits a seasonal decline in catches, to a low in October of 9 and 42 ind/tow, in Groups 2 and 3, respectively. Group 1 catches of *B. glaciale* were substantial only in February (67 ind/tow). Two animals were captured in two of five Group 1 stations in December, four animals were captured at one of seven Group 1 stations in October and none were sampled in Group 1 in June.

Notolepis rissoi has a subpolar-temperate distribution, based on similarities between its geographic range and *B. glaciale* (Backus et al. 1970). Catches of *N. rissoi* in Groups 2 and 3 were similar, except in June and August. The largest catches of *N. rissoi* occurred in Group 2 stations in June (111 ind/tow). *Notolepis rissoi* was only found in Group 1 stations in February. Seasonality was not marked although higher abundance was indicated in the June and August samples.

4.4 Discussion

Ordination and classification of species abundance data demonstrated spatial variability and seasonal changes in species composition and relative abundance of mesopelagic fish species in the Slope Sea off Nova Scotia. Between 63 and 73% of the variability in species composition was associated with one major gradient. Geographically, this gradient lay in a south-north direction and correlated with decreasing bottom depth, surface and subsurface temperature, and surface salinity. Within each survey, the station groups formed by classification differed in faunal characteristics such that the groups comprising the southern stations exhibited the highest values of species richness and greatest equatability in relative abundance, while the groups composed of more northern stations were consistently less rich in species, with greater unevenness.

Fit between station groups and water masses was better for some surveys than others as groups were usually, though not always, coherent in terms of their hydrographic characteristics. Presence of WCR samples enhanced the fit by polarizing the stations and increasing the lengths of the gradients. Misclassified stations were always very close to the subsurface fronts (though not all frontal stations were misclassified) and exhibited the lower species richness and particular dominant species typical of stations on the landward side of the front. Sites from the LSW and WSW were most similar in February, and hence the highest proportion of misclassified sites occurred in that month, but misclassified sites occurred in April and October also. Although the classification formed station groups which were generally congruent with the water masses, close inspection of the two-way tables reveals few disjunctions in the occurrence of species across the hydrographic fronts. Group 1 always contained a number of exclusive species but, except in the WCR samples from June, these were species of low abundance. Most species occurred in two and sometimes all three stations groups. Two of the most abundant species exhibited a lack of uniformity in abundance across the LSW/WSW boundary. *Benthosema glaciale* was generally much less abundant in the WSW than the LSW, and the reverse was true of *C. maderensis*. The distance separating adjacent station groups on the ordination axes was usually narrower than the width of the station group indicating that the variability in species composition and abundance within a group was frequently as great as between two adjacent station groups. The two way tables show that species exhibit individual responses to the gradient. Therefore, station groups differed in species richness, evenness of abundance and species composition but the fauna associated with them intergrade into each other.

April and June surveys were exceptional in that several numerically abundant species only occurred in one station group; the WCR stations forming Group 1 in June and the WSW stations of Group 2 in April. Ordination diagrams for these two surveys showed relatively large gaps present between the station groups. The possibility that this was an artifact of sampling caused by the widely placed sampling sites in both surveys was considered since classification of samples collected irregularly from a gradient of continuous faunal turnover can cause artificial clusters. For example, WCR and WSW stations were more closely placed in the December survey and the ranking species were similar in both groups. However, the fauna of a WCR will vary, depending on factors such as the season in which the ring formed, its size, and the degree of interaction between it and the WSW or GS. The WCR sampled in June was probably newly formed, whereas the WCR sampled in December had been interacting with the WSW, based upon the absence of *C. maderensis* in the former. In April, stations comprising Groups 1 and 2 were also separated by distances exceeding 75 miles, but the member stations were also widely separated, indicating that faunal differences did not rise solely from sampling.

TWINSPAN and PSi stressed different aspects of the faunal structure in their separation of stations. TWINSPAN ordered stations along a gradient of decreasing species richness, and the divisions seemed related to the presence or absence of species of medium abundance, while the PSi primarily grouped samples on the basis of the dominant species. Agreement between the two methods was generally good except for the February and October surveys. Comparing classifications of these two surveys, PSi was more effective in classifying the February survey, but less effective than TWINSPAN with the October survey. This suggests that TWINSPAN is a better method by which to classify samples with high species richness and evenness but it may obscure the affinities between relatively similar samples of low diversity.

The lack of disjunct species distributions associated with the fronts indicates that the positions of the subsurface water masses are not sufficient to explain species composition. Although there may be factors associated with the water masses which limit species distributions, any resulting patterns are obscured by continuous mixing between adjacent faunas due to movements of the major hydrographic fronts, rings, and entrainment of SHW and WSW by rings and the GS. Rings may be the primary transporter of subtropical and tropical species into the WSW (Craddock et al. 1992), but in general, fronts are transition areas rather than barriers to the movement of plants and animals (McGowan 1974; Brandt 1981; Brandt and Wadley 1981). The effects of mixing on faunal composition are apparent in the October survey where stations sampled in the WSW interleaving with LSW landward of the primary LSW/WSW fronts displayed a species composition similar to that of LSW stations.

The gradient in species diversity observed between the southern and northern stations would be anticipated because of their proximity to very different faunal regions. The subarctic and subtropical faunal regions have relatively very low and high species richness, respectively (Backus et al. 1977), so faunal richness in the WSW should decrease with distance from the boundary between the WSW and GS. This gradient may have been accentuated by the frequent occurrence of rings at the southern end of the eastern transect in contrast to the mixing between WSW and LSW observed at the northwestern stations (Halliday et al. 1995).

Increase in species richness and evenness from the winter-spring to summer-fall surveys is related to seasonal cycles in abundance for five of the eight species abundant in the WSW that are also abundant in the Sargasso Sea. Of these, *L. guentheri, L. dofleini, H. hygomii*, and *C. warmingii* have one year life cycles with the maximum abundance of animals > 20 mm occurring in the late spring through fall, and the fifth, *Notoscopelus resplendens*, although it has a two year life cycle, also shows a peak in abundance in late spring (juveniles

<31 mm) and a decline to very low levels in late summer and winter (Karnella 1987). It is assumed here that occurrences of these species in the WSW are due to immigration from breeding populations in tropical and subtropical regions, based on their greater relative abundance in these locales (Backus et al. 1977), and the absence or infrequent occurrence of their larvae in the WSW (Chapter 5). As no seasonal signal has been observed in the frequency of WCR formation or position in the WSW (K. Drinkwater, Bedford Institute of Oceanography, Dartmouth, N.S; personal communication) the rate of transport can be assumed to be constant or irregular. Thus, the occurrence of a subtropical or tropical species in the WSW is determined only by the timing of its lifecycle in the Sargasso or Caribbean Seas, as the transport mechanism into the WSW is not variable seasonally.

Three abundant species do not conform to this explanation for a seasonal pattern in species richness in the WSW. *Benthosema glaciale* lives longer than two years in the Northwest Atlantic (Halliday 1970), but its abundance in the WSW declined from April to October. Its average density in the WSW during those months was 7-17 % of that in the LSW. In contrast, the density of *C. maderensis* which lives about two years (Linkowski et al. 1993), was fairly constant in the WSW over the same period. Both of these species breed in the WSW (Morse et al. 1987; Chapter 5). The third species, *H. benoiti*, a spawning resident of the Sargasso Sea, reaches its greatest abundance there in the winter (Karnella 1987). If its occurrence in WSW is solely related to its seasonal pattern of abundance and transport from other regions, it should have occurred throughout the WSW sites, and at some of the LSW sites in February and April. Instead, the only stations at which more than one *H. benoiti* were captured were the five most southwestern WSW stations (Group 1) in February, and four WSW and one LSW station in April.

The cold, surface layer of SHW which occurs in winter is considered as the cause of lower species richness in the February and April surveys, based on comparisons of the vertical thermal structure of the Sargasso Sea, WSW and LSW. Jahn (1976) explained seasonal and geographic differences in faunal composition and diversity between WSW, Cold Core Ring and Sargasso Sea stations, by describing the midwater environment as a two layer model. Physical conditions in the surface (upper 200 m) and deeper layer differ between the Slope Water and Sargasso Sea. The upper layer of the Slope Water lying just above the main thermocline, undergoes winter cooling to temperatures < 10 °C while temperatures in the deeper (>200 m) layer are 5-10 °C. In contrast, in the Sargasso Sea the thermocline is below 900 m (below the day time depth of many vertically migrating species) and thus many species living there never experience temperatures < 10 °C. The surface layer of the Sargasso Sea is always > 18 °C even in winter months. The occurrence of species in either habitat (Slope Water or Sargasso Sea), or in cold core rings was determined by their response to the temperatures in both vertical layers. He concluded that the surface layer of the Slope Water would be within the physical tolerances of species from the Sargasso Sea during summer months, but not in the winter.

Physical conditions in the WSW and LSW during the surveys can be compared using the same model. The range in temperature below 200 m in the WSW (14.5-4.7 °C) was broader than in the LSW (8.9-4.2 °C). The surface layer of both water masses was seasonally variable with the coldest temperatures occurring in April (Table 4.2). Also, part of the WSW was covered by the SHW. This layer was variable in position, with the front occurring furthest south of the subsurface LSW/WSW front during the winter surveys, and over the front in the summer surveys.

Since the LSW, WSW and GS continuously exchange water and fauna, the WSW will contain native species as well as primarily subtropical, tropical (warmwater) and subarctic (coldwater) species from the bordering regions. As surface temperatures decline during the winter, vertically migrating warmwater species will encounter cold temperatures in the surface layer, particularly areas overlain by the SHW. If these species could adjust their vertical range to avoid the surface layer or if they die because they are cut off from the productive surface layers, species richness and evenness will decrease (or appear to in night samples within the 0-200 m layer), and faunal composition will resemble samples from the LSW. As surface temperatures in the WSW rise, conditions would favour warmwater species over coldwater species; species richness and evenness would rise and the faunal composition will be more similar to WCR samples than the LSW. However, the numbers of warmwater species and therefore species diversity would also rise in the LSW with the increase in surface temperatures during the summer.

Seasonal cooling by the WSW surface layers would reinforce the decline in the abundance of the subtropical species, already discussed in relation to their one year life cycle. The model explains why none of these species appear to have self-sustaining populations in the WSW (Chapter 5), although they thrive there in the summer months. They may be able to survive in the southernmost part of the WSW, but they would be progressively excluded from the more landward part, and must recolonize each year. *Hygophum benoiti* did not occur at the WSW stations which exhibited cold surface temperatures because it prefers the surface or very shallow depths at night ((Karnella 1987; Gartner et al. 1989; Linkowski 1996). Decreasing abundance of *Benthosema glaciale* in the WSW during the summer can also be rationalized by this model. This species does not vertically migrate in the Sargasso Sea or in cold core rings (Karnella 1987; Backus and Craddock 1982). In the latter, their abundance decreased and their depth of occurrence deepened as the depth to 15 °C increased from 200 to 515 m. This behaviour may be a response to too warm surface conditions (Wiebe and Boyd 1978) or low zooplankton concentrations associated with the warmer water (Sameoto 1988), and eventually leads to starvation (Boyd et al. 1978). *Benthosema glaciale* may react to the high surface temperatures of the WSW of August and October in a similar manner, as suggested by decreasing abundance of age 1+ individuals, and the decreasing proportion of them vertically migrating (Chapter 3).

Other studies have also associated surface water characteristics with community composition. Robison (1972) related decreasing species richness between the southern and northern parts of the Gulf of California to the occurrence of warmer high-salinity surface water in the latter region. The distribution of mesopelagic species in and around warm core eddies off East Australia is very similar to that occurring in the Slope Sea as species were alternatively confined to eddies, only occurred outside of eddies, or were ubiquitous (Brandt 1981). Brandt found that species were very specific about the thermal regimes they inhabited and suggested that this specificity contributed to the maintenance of differences in assemblages inside and outside the eddy. Paxton (1967) argued that seasonal changes in mesopelagic fish abundance off California were not due to the surface environment becoming more favourable to northern or southern species, because abundance cycles for all species coincided. Instead, he suggested that either food or predation became limiting, or active or passive migration increased during the summer months. However, abundance cycles in the WSW do not coincide (Chapter 2), supporting the hypothesis that surface environmental conditions favour subarctic species in the winter and subtropical species in the summer.

Previous studies in the Slope Sea also found differences in faunal composition and structure associated with stations either partitioned arbitrarily by water mass (Jahn and Backus 1976, Backus and Craddock 1982), or through multivariate analyses (Jahn 1976, Jahn and Backus 1976, McKelvie 1985a). These studies were short term or single surveys, and as shown in Chapter 2, their descriptions of the fauna were only adequate for that month or that portion of the Slope Sea. The present study is unique in providing systematic seasonal sampling which demonstrates the dynamic aspects of changes in species distributions and abundances.

Chapter 5: The nature of the fauna of the Warm Slope Water

The objective of this study was to determine whether the Slope Sea supported a characteristic and persistent fauna, or was only a transition zone between a coldwater (subarctic) and warmwater (subtropical) fauna. Results from repeated large-scale sampling showed a diverse fauna dominated by a few very abundant species. The relative abundance of these dominant species varied seasonally, but were consistent with sampling by other studies in the Slope Sea in a given season. The assemblages within the three water masses sampled (LSW, WSW and GS/WCR) were distinguishable from each other by differences in their species richness, evenness of abundance and ranking species. The approach taken in Chapter 2 was to compare assemblage structure after pooling samples based on hydrographic characteristics at sampling locations. Results from this method can be misleading since, if species distributions form a continuum across the area sampled, pooling samples by water mass could obscure the overall similarity, depending on the distribution of sampling along the gradient. Classifying stations by their species composition (Chapter 4) also indicated distinct differences corresponding to water masses, but the situation was complex since within a cruise, faunal characteristics of stations near the hydrographic fronts were sometimes more similar to those in the adjacent water mass than to stations with similar hydrography. Among cruises, structure of the assemblages varied so that greater similarity between stations in two adjacent water masses occurred in some months than in others. Few species had disjunct distributions across the hydrographic fronts but some had large discontinuities in abundance so that faunal differences between water masses resulted from changes in abundance rather than presence or absence. Analysis of the distributional data demonstrated that faunal composition was neither homogenous within the water masses (with abrupt shifts in fauna occurring at the boundaries), nor so gradual in its transformation across the water masses that the boundaries could not be perceived in the species composition data.

Communities (or assemblages) are groups of species occurring together in space and time and presumed to be functionally interacting with each other and with the environment (Mills 1969). Recognizable boundaries between adjacent communities, such as by rapid faunal changes (Haedrich et al. 1980), are seen as an exception rather than a rule, as most communities grade into each other (Begon et al. 1990). Thus, the lack of disjunct species distributions across the hydrographic fronts defining the WSW is not evidence that there is no distinctive assemblage associated with the WSW. McKelvie's (1985a) conclusion that the WSW is only a transition zone because it contained elements of the adjacent faunas is erroneous since there are other features which indicate that the fauna is distinctive. In particular, the centre of abundance of *Ceratoscopelus maderensis* is in the WSW, and high relative abundance of other species suggests that some of the ranking species may maintain self-reproducing populations in this region. Van der Spoel (1994a,b) argues that locally isolated ecosystems do not occur in the open ocean, because ecological processes there are more dependent on outside influences than local ones, therefore 'the pelagic environment consists solely of ecotones'. The consistency in faunal composition between this study and previous surveys suggests that there is a persistent assemblage. The interesting questions are: what are the processes shaping this assemblage, and how much of its structure is due to extrinsic factors?

Processes which affect the structure of assemblages can be classified as deterministic or stochastic. Deterministic interactions, both physical and biological, are important in predictable or constant environments, and are reflected in observations of persistent, stable assemblages. Stochastic interactions are unpredictable events, such as the advection of water bodies and fauna as a result of storms, resulting in variability in assemblage structure (Grossman 1982; Grossman et al. 1982). Community structure within some tropical regions is so constant as to indicate that biological interactions are very important (McGowan 1974; Barnett 1983, 1984; Clarke 1973; 1974; Gartner et al. 1987). Barnett (1983) suggests that the large gyres of the North and South Pacific are regions of such physical homogeneity and low advection, as to be semi-enclosed systems. In contrast, a tremendous amount of mixing of water and fauna occurs at the boundaries of the gyres so that advective events are as or more important than any biological interactions in shaping community structure. These regions are regulated by both physical and biological interactions such as occur in the centre of the gyres, and variable and large-scale horizontal advection.

Measures of community structure can be used to determine the relative importance of deterministic and stochastic events. McGowan (1977) illustrates useful indices by comparisons between the North and South Pacific Gyres, which are self-regulated systems, and the California Current, which is a transitional area with a characteristic fauna of species with transitional water, subarctic and subtropical-tropical distribution patterns (Berry and Perkins 1966; McGowan 1974, 1977). Self-regulated systems should display low heterogeneity in biomass, constant species composition and high frequency of occurrence, stable rank orders of dominance (e.g. large PSi's) and high evenness of abundance. Comparisons among these regions with the WSW suggest that the WSW is intermediate between the California Current and gyres. The fauna of the WSW is more predictable than that the California Current but the median PSi is well below those of the North Central Gyre (Table 5.1). Abundance was also more unevenly distributed amongst species in the WSW than in the gyres. Thus, the processes determining the structure of the WSW assemblage are more predictable than they are in the California Current.

Three interacting mechanisms were proposed in Chapter 4 to explain species distributions and faunal composition within the Slope Sea. These were 1) continuous advection of fauna into the Slope Sea by the Labrador Current

Table 5.1. Comparison of sampling effort, species richness and Percent Similarity Indices (PSi) for trawl samples from the North and South Pacific Gyres and California Current (from Barnett 1983), and the Warm Slope Water (PSi for Slope Water based on 20 samples from October, cruise N110, a- from Berry and Perkins 1966).

Location	No.of species/ No. of samples	Median PSi	Range PSi	% Evenness (top n species)
North Central Gyre	228/117	63.9-64.6	42.9-81.7	59 (5)
South Central Gyre	144/15	55.5-75.0	51.6-67.3	58 (5)
California Current	189/198[a]	42.87	1.0-92.75	52 (2)[a]
Warm Slope Water	214/147	49.7	14.8-88.5	58 (2)/79 (5)

(subarctic fauna) and warm core rings (subtropical/tropical fauna); 2) several abundant species live only one year and so have seasonal cycles of abundance; 3) seasonal cooling of the surface layer of the WSW in winter decreases its suitability for subtropical species. This last mechanism would affect the reproductive success of any subtropical species spawning in the WSW, requiring them to re-colonize this region most years.

The fauna can be divided into rare (< 16 individuals total), common (17-500) and abundant (>500) species. Most of the 227 species collected occurred so infrequently that their capture supplies no life history information other than range extensions. Existing distributional information on the rare species (63 % of the total fauna) indicates that many may are expatriated from subtropical and tropical regions (Chapter 2), for example, the fifty percent which were myctophids or stomiatoids were previously found mainly south of the study area (Nafpaktitis et al. 1977; Gibbs 1984a,b,c,d). The sixty common species are a mixed group. Some elements are obviously expatriated from subtropical regions, while others are wide-ranging species which may have self-sustaining populations. The mesopelagic zone was defined in this study as if the lower limit (1000 m) was a barrier, but it is as vague a boundary to vertical migration of many species as hydrographic fronts are to horizontal migration (van der Spoel 1994b). While some species were easily excluded by this depth criterion (eg. ceratioids), others such as melamphaids use the mesopelagic zone as juveniles but migrate into it less frequently as adults

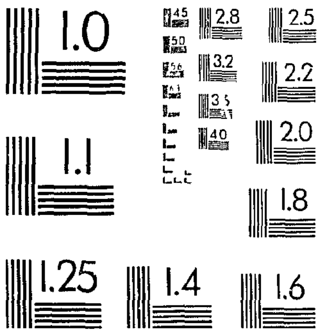
(Maul 1986). Thus, some species belonging to the common group probably have native populations which were not comprehensively sampled because of bathypelagic or neustonic (discussed in Chapter 2) life stages. The abundant species are the 25 top-ranking species (Table 2.3, standard surveys). Fourteen of those (ranked seventh to twenty-fifth) are species whose occurrences can be linked to spawning populations in subtropical and tropical regions (Backus et al. 1977; Gartner et al. 1987; Karnella 1987; Lancraft et al. 1988; Howell and Krueger 1987; Gartner 1993). Four of the remaining species (*Chauliodus sloani, Stomias boa, Nemichthys scolopaceus* and *Serrivomer beanii*) probably have native populations in the Slope Sea, judging by their frequency in trawl samples from the shelf edge and slope (McKelvie and Haedrich 1985; Scott and Scott 1988). The seventh ranked species, *Cyclothone* was a species complex of which at least two spawn in the Sargasso Sea (Bond 1974, cited by McKelvie 1989) and are highly ranked species in the WSW (Craddock et al. 1993). The abundance of *Notolepis rissoi* (ranked sixth) in trawls on the shelf edge and slope, and the frequent occurrence of postlarvae (Scott and Scott 1988; Chapter 3) indicated that it is also native.

The five top-ranked species, *C. maderensis, B. glaciale, Lobianchia dofleini, Hygophum hygomii* and *N. resplendens,* are important members of the Slope Sea fauna, comprising over 75% of the total numbers caught. These species are also important members of the fauna in other regions of the North Atlantic. *Benthosema glaciale, C. maderensis, L. dofleini* and *H. hygomii* coexist and spawn in the Mediterranean Sea and *B. glaciale*, *C. maderensis*, and *N. resplendens*, in the Mauritanian upwelling (Goodyear et al. 1972; Palomera and Rubies 1982; Badcock 1981; Sabates 1991). Some evidence is available to indicate whether the source populations of these species occur in the WSW, specifically their centres of abundance, larval and juvenile occurrences in the Tucker trawl surveys and in published ichthyoplankton surveys of the WSW.

There is ample evidence that *C. maderensis* and *B. glaciale* have self sustaining populations in the WSW. Numerous *C. maderensis* larvae (5-16 mm) have been captured in ichthyoplankton surveys of the WSW off Nova Scotia (Evseenko 1982; unpublished data, Marine Fish Division, Bedford Institute of Oceanography, Box 1006, Dartmouth, N.S., B2Y 4A2) and between the Gulf of Maine and Cape Hatteras (Morse et al. 1987; Cowen et al. 1993), and larvae and juveniles were abundant in Tucker trawl samples from August. The large numbers which sometimes occur in samples from the Gulf Stream and Sargasso Sea (Jahn and Backus 1976; Gibbs et al. 1971) are individuals expatriated from the Slope Sea (Jahn 1976; Karnella 1987). Its low relative abundance in samples from the Subarctic region (Backus et al. 1977; McKelvie 1985b) suggests that these animals are also the result of expatriation. Occurrences of *B. glaciale* in the Sargasso Sea are also due to advection by cold core rings from the Slope Water, and its distribution there is limited to depths > 500 m (Backus and Craddock 1982; Karnella 1987). *Benthosema glaciale* larvae (3-11 mm) regularly occurred over several years in samples taken at the edge

3 OF/DE 3

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



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of the continental shelf between the Gulf of Maine and Cape Hatteras in WSW (Morse et al. 1987) as well as near the Scotian Shelf (unpublished data, Marine Fish Division). A few postlarvae (9-10 mm) were taken in Tucker trawl tows in June in WSW and postmetamorphic individuals were abundant in August (Chapter 3). The decline in abundance of age-1+ *B. glaciale* in the WSW between winter and fall IYGPT surveys, and between April and August Tucker trawl samples may be due to an exodus of older individuals from the WSW (or death), or a large proportion of them ceasing vertical migration. It was suggested in Chapters 2 and 3 that conditions become less favourable to coldwater species such as *B. glaciale*; as surface temperatures warm, they are excluded from the shallow depths where zooplankton concentrations are highest (Sameoto 1988).

Evidence to indicate that the abundance of *L. dofleini, H. hygomii* and *N. resplendens* is due to spawning populations in the Slope Sea, rather than expatriation from the Sargasso Sea is weak. These species are top-ranking species off Bermuda and spawn there, based on the occurrence of gravid females and larval captures (Karnella 1987). Karnella and Gibbs (1977) argue that the high density of *L. dofleini* off the continental shelf of the United States and the capture of 12 mm juveniles off Cape Hatteras indicate that the species spawns in the WSW. However, few small *L. dofleini* individuals (<26 mm) were collected in Tucker trawl samples. There is no information indicating larval occurrences of the three species in ichthyoplankton surveys of the slope.

The only exceptions are eight *H. hygomii* larvae (4.2-6.4 mm) collected in the Slope Sea off Nova Scotia, but these were taken in water with Gulf Stream characteristics (Evseenko 1982) suggesting that a WCR was sampled. If the three species were spawning in WSW, large numbers of small juveniles would be anticipated in the Tucker trawl samples, as were observed for *B. glaciale* in June and *C. maderensis* in August (Chapter 3).

In summary, *B. glaciale, C. maderensis* and *N. rissoi* have self sustaining populations in the Slope Sea, based on the occurrence of postlarvae and juveniles, and the occurrence of adults year round. *Lobianchia dofleini, H. hygomii* and *N. resplendens* are plentiful in the WSW between June and October, but the lack of larval captures in ichthyoplankton surveys or small juveniles in Tucker trawl samples suggest that these three species could be sustaining large populations seasonally entirely through immigration into the WSW from the Sargasso Sea. More evidence is required, such as the presence of gravid females and larval records, to resolve this question.

The richness of the mesopelagic fauna of the WSW can be attributed to advection of water and fauna from the GS and Labrador Current. If some of the most abundant species are there due to input from adjacent regions, then rates of advection and mixing must be very high. Advection has two effects: 1) contribution of fauna and 2) modification of the physical oceanography of the region. The influence of the GS is easy to observe, since WCRs carry a diverse array of southern species. Backus (1987) suggests that the fauna of the westernmost portion of WSW differs from the rest of the region because rings frequently occur there, renewing the warmwater species and also modifying the habitat. The contribution by the Labrador Current is less obvious, since its fauna is relatively impoverished, and its dominant species (*B. glaciale*) is already a self sustaining member of the WSW fauna. Petrie and Drinkwater (1993) noted a fourfold variation in the rate of water transport by the Labrador Current along the Scotian Shelf between 1945 and 1990, and attributed a trend of cooling and freshening of waters over the slope to the years when transport rates were highest. Conditions in the WSW may be favourable to coldwater species in years when the rate of transport is high, while warmwater species may successfully colonize the WSW during those periods when transport rates are low.

The high species richness of the Slope Sea (227 species, 68 myctophid species) is comparable to that found in low latitude oceanic systems such as the North Pacific Gyre (250 species, Barnett 1983) or eastern Gulf of Mexico (50 myctophid species, Hopkins and Gartner 1992), and contrary to the generalization that the species diversity of marine plankton decreases from low to high latitude systems. Hopkins and Gartner (1992) attribute the diversity of the Gulf of Mexico ecosystem to partitioning of vertical space and food resources brought about by diffuse competition, which they define as the effect of combined competition from all other species at that trophic level. In contrast, I suggest that the diversity of the Slope Sea is maintained by repeated disturbance in the form of advection and mixing, which create a non-equilibrium situation (Huston 1979). Under these conditions, competitive exclusion would not occur because 1) population rates are kept low so that species never reach densities at which they are in competition for resources and 2) physical conditions are so variable that situations in which one species has a competitive advantage over another are very brief (Huston 1979). Thus, biological interactions such as competition are likely to be unimportant in maintaining the richness of the mesopelagic fish assemblage inhabiting the WSW, at least in contrast to the effects of physical transport.

The WSW was recognized as a pelagic faunal province of the North Atlantic Temperate Region in the zoogeographic system developed by Backus et al. (1977). Although the temperate region is narrow in the western North Atlantic, it covers much of the eastern portion, extending from north of Scotland (60°N) to North Africa and including the Mediterranean Sea. The WSW is geographically isolated from the rest of the temperate region and its connection partially restricted by the influences of the Labrador Current and Gulf Stream. However, it should have a characteristic fauna due to this connection to the larger faunal region. The doubt over the distinctiveness of the WSW fauna has risen from the narrowness of this province, and hence, the relatively important scale of boundary effects.

Appendix 1. Deep bathypelagic, epipelagic and neritic species captured with an IYGPT or Tucker trawl during the ten mesopelagic surveys of the Slope Sea between 1984 and 1989.

Name	Frequency	Total
Petromyzon marinus	3	3
Etmopterus princeps	4	4
Albula vulpes	1	1
Aldrovandia phalacra	1	1
Halosaurid sp.	1	1
Notacanthid sp.	1	1
Anguilla rostrata	17	41
Gymnothorax sp.	4	4
Muraenid sp.	1	1
Ahlia egmontis	7	21
Myrophis punctatus	3	8
Ophichthus cruentifer	5	8
Facciolella sp.	5	5
Hoplunnis sp.	5	6
Nettastoma sp.	1	1
Ariosoma balearicum	1	1
Ariosoma sp.	16	49
Congrid sp.	134	723
Hildebrandia sp.	1	2
Paraxenomystax sp.	18	27
Uroconger sp.	1	5
Etrumeus teres	1	45
Engraulis eurystole	3	3
Glossanodon sp.	8	10
Alepocephalus sp.	2	2
Einara edentula	1	1
Photostylus pycnopterus	2	2
Rouleina maderensis	1	1
Xenodermichthys copei	1	1
Holtbyrnia anomala	3	3
Normichthys operosus	13	24
Searsia koefoedi	4	4
Ahliesaurus berryi	4	5
Scopelosaurus argenteus	1	1
Scopelosaurus lepidus	33	53
Scopelosaurus mauli	1	2
Scopelosaurus smithii	5	11
Synodontid sp.	5	103

Appendix 1 cont.

Name	Frequency	Total
Trachinocephalus myops	6	8
Alepisaurus ferox	6	7
Laemonema barbatula	5	7
Morid sp.	6	9
Svetovidovia sp.	19	59
Bregmaceros sp.	50	83
Gadus morhua	2	2
Phycis chesteri	29	63
Urophycis tenuis	6	10
Urophycis sp.	1	2
Macrourid sp.	10	12
Nezumia bairdi	3	3
Carapid sp.	8	11
Echiodon dawsoni	6	6
Antennarius sp.	3	3
Histrio histrio	2	2
Dibranchus atlanticus	3	3
Cryptopsaras couesi	55	80
Cryptopsaras sp.	1	1
Edriolychnus schmidti	5	5
Linophryne brevibarbis	1	1
Linophryne coronata	1	1
Linophryne macrodon	1	1
Linophryne sp.	1	1
Linophrynid sp.	2	3
Danaphryne nigrifilis	1	1
Lophodolus acanthognathus	2	2
Oneirodes sp.	1	1
Oneirodid sp.	4	6
Lasiognathus beebei	1	1
Himantolophus sp.	5	5
Melanocetus johnsoni	5	5
Melanocetus murrayi	2	2
Scomberesox saurus	7	10
Beryx decadactylus	2	2
Beryx splendens	2	2
Polymixia lowei	5	6
Fistularia tabacaria	5	5
Macrorhamphosus scolopax	1	1
Hippocampus erectus	5	6
Ectreposebastes imus	2	3
Helicolenus dactylopterus	20	42
Sebastes mentella	1	1

Appendix 1 cont.

Name	Frequency	Total
Sebastes sp	18	69
Scorpaenid sp.	4	5
Anthias sp.	11	22
Epinephelus sp.	7	14
Gonioplectrus sp.	1	1
Serranid sp.	2	3
Serranus sp.	1	1
Symphysanodon sp.	2	3
Rypticus sp.	2	2
Percoid sp.	49	252
Cookeolus boops	1	1
Priacanthus arenatus	6	12
Lopholatilus chamaeleonticeps	1	1
Caranx hippos	1	1
Caranx sp.	3	5
Decapterus sp.	2	2
Naucrates ductor	1	1
Selar boops	1	1
Selar crumenophthalmus	1	1
Selene vomer	9	14
Taractes asper	1	1
Taractes sp.	1	1
Taractichthys longipinnis	2	2
Chaetodon sp.	6	7
Holocanthus sp.	13	26
Labrid sp.	5	5
Mugil cephalus	1	1
Mugil curema	1	1
Melanostigma atlanticum	1	5
Callionymus agassizi	5	5
Callionymid sp.	2	3
Acanthurus sp.	14	41
Tetragonurus atlanticus	3	3
Peprilus triacanthus	5	8
Bothus sp.	48	121
Citharichthys arctifrons	8	11
Etropus microstomus	1	1
Monolene sessilicauda	1	1
Trichopsetta sp.	3	4
Glyptocephalus cynoglossus	2	3
Symphurus sp.	2	2
Stephanolepis hispidus	15	19
Sphoeroides maculatus	3	3

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