



JOCK YOUNG, *Hippolyte Rock, S.E. Tasmania* 1994, oil on linen, 61 x 121.5cm

**ECOLOGY OF MIDWATER ZOOPLANKTON AND
FISHES OFF EASTERN TASMANIA, AUSTRALIA**

by

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Submitted in fulfilment of the requirements
for the degree of
Doctor of Philosophy

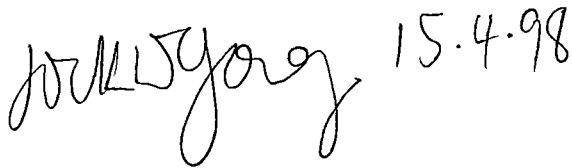
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ABSTRACT

This thesis examines the ecology of zooplankton, midwater fishes and top predators off the east coast of Tasmania in relation to the regional oceanography. This work was completed from small (<15 m) to large (60 + m) fishing and fisheries research vessels using nets ranging from fine-meshed plankton nets (100 μ m) to large midwater trawls (cod end mesh size 10 mm). Further data was obtained from the Maria Island hydrographic station and the AFZ observer program.

The study area was situated in and around the northern edge of the subtropical convergence zone. This zone separates the most southern edge of the East Australia Current from the broader subtropical convergence and subantarctic water to the south. The latitudinal position of this front depends not only on the time of year — in the summer it extends southward and retreats in winter — but also on interannual cycles such as the El Nino Southern Oscillation.

On the shelf the distribution and biomass of the major zooplankton species, *Nyctiphanes australis*, was closely related to fluctuations in these water masses. This species is central to the shelf food web — it is, at times, the main prey for predators ranging in size from larval fishes (eg. those of jack mackerel *Trachurus declivis*) to large southern bluefin tuna (*Thunnus maccoyii*). In autumn, when its biomass is highest, schools of its main fish predator, jack mackerel form on the surface over the shelf where they are fished commercially. The central position of *N. australis* in the shelf food web was demonstrated in the summer of 1988/89 when warm waters from an anti El Nino event flushed the shelf resulting in the disappearance of the krill and the subsequent collapse of the jack mackerel fishery.

Over the continental slope a suite of myctophid species dominated the water column. These lanternfish aggregate in dense schools over the slope in spring and summer, migrating to the surface at dusk and descending before dawn to depths between 300–500 m. Their horizontal distribution is restricted mainly to a thin band (~500 m wide) over the 300 m contour. One of these, *Lampanyctodes hectoris*, was central to the upper slope food web. Examination of the reproductive cycles of *L. hectoris* and other abundant lanternfish showed multiple spawning over winter. The winter spawning is presumably timed so that juveniles can take advantage of increased prey

levels, mainly euphausiids, which are generated by the spring bloom. Growth in *L. hectoris*, which lives up to 3 years, is fastest at this time. In winter they are scarce over the slope. The reasons for this scarcity are not clear, but it is at least partly due to the massive predation on them. However, lack of feed — copepods are the main prey over winter — may limit the size of aggregations that can be sustained. The concentrations of lanternfishes during spring and summer form the basis of a food chain supporting larger fishes such as blue grenadier (*Macruronus novaezelandiae*) and jack mackerel, and during summer, other larger lanternfish such as *Diaphus danae*.

Offshore, a more diverse community of midwater fishes was identified, which, although similar among the different water masses, was significantly different in the surface waters of the East Australia Current, the result of a relative increase in species of subtropical origin. Densities were an order of magnitude lower than that found for the slope lanternfish. The diets of lanternfish offshore were dominated by calanoid copepods, particularly those of the genus *Plueromamma*. Non-mycetophids within the same size range ate a wider range of prey. Some, such as the Stomiatoidei genus *Chauliodus*, were entirely piscivorous on lanternfish.

Estimation of the relative biomass of zooplankton and micronekton from the main geographic and oceanographic regions of the area showed that shelf biomass was significantly higher than that offshore. This increased biomass appears to be derived from a mixture of subtropical convergence water washing over the shelf and shelf-break upwelling. The higher biomass over the shelf was reflected in the daily ration of shelf-caught southern bluefin tuna (*Thunnus maccoyii*), which fed mainly on jack mackerel and had rations ~3 times that of offshore-caught tuna.

I identified 10 trophic categories off eastern Tasmania across the shelf to the open sea. These were — large pelagic omnivores (eg. *Thunnus maccoyii*), pelagic omnivores (eg. *Trachurus declivis*), pelagic piscivores (eg. *Brama brama*), small mesopelagic omnivores (eg. *Diaphus danae*, *Lampanyctus australis* and *Chauliodus sloanii*), neritic planktivores (eg. *Lampanyctodes hectoris*), bathypelagic omnivores (eg. *Hoplostethus atlanticus*), squid (eg. *Nototodarus gouldii*), gelatinous zooplankton (eg. *Pyrosoma pyrosoma*), oceanic (eg. *Pleuromamma* spp. and *Phronima sedentaria*) and shelf (eg. *Nyctiphanes australis*) zooplankton.

A common theme, which has run through many of these studies, was the link between inshore and offshore processes. Although the dominant zooplankton and micronekton species were usually restricted in their distributions (eg. *Nyctiphanes australis* with the shelf), their main predators moved freely between the inshore and offshore waters. I believe that the movements of these predators are determined largely by prey availability. Thus, prey availability, itself dependent upon seasonal and interannual cycles in the regional oceanography, appears to drive much of the seasonal and interannual patterns of abundance of larger fishes in the region. Two of these species, jack mackerel and southern bluefin tuna, are the focus of commercial fisheries. Their effective management therefore will need to consider (1) the dependence of the tuna on the mackerel and (2) that both species in this area depend, either directly or indirectly on krill stocks, which in turn depend on the fluctuations of the regional oceanography.

Finally, over the period of this study there have been a number of advances both in techniques and technologies in the study of midwater communities. I have therefore summarised those techniques and approaches to studying the midwater that I think have benefited this area of research. I have also identified some of the difficulties that need addressing.

ACKNOWLEDGMENTS

This thesis is the result of work I have completed over ten years working as a marine biologist with CSIRO Division of Fisheries in Hobart, Tasmania (now Division of Marine Research). All of the work has resulted from trips to sea along the coast of Tasmania. By its very nature working at sea requires a good deal of teamwork and this thesis would not have been possible without the efforts of the many people involved, far too many to list here. However, there are some that need mention. I would like to thank the captains and crews of Fisheries Research Vessels *Scottsman*, *Challenger*, *Soela* and *Southern Surveyor* with a special thanks to the fishing master of *Southern Surveyor*, Roger Pepper. I would also like to thank Dr Steve Blaber who led the original “Southern Program” study; Drs Vincent Lyne and Graham Harris, Mr Brian Griffiths and Ms Leslie Clementson who helped me understand the complexities of the physical and biological oceanography of the area. Dr Bob Johannes started me on the krill project and Alan Jordan provided enthusiasm and expertise in that field. Special thanks to Tim Lamb and Russ Bradford for their contribution to the offshore component of the project, and Wade Whitelaw for his role in liaising with the AFZ Observers.

The published papers were the result of many revisions and I am indebted for the initial guidance offered by Drs Roy Harden Jones (former chief of CSIRO Division of Fisheries) and Vivienne Mawson. I have taken care to include as co-authors all those people who have materially helped in the resulting publications, primarily technical staff and line managers but also people from other organizations with whom I have collaborated. The latter are Dr R. Rose, University of Tasmania; Messrs Alan Jordan and Grant Pullen, Tasmanian Department of Sea Fisheries. However, the results obtained and conclusions drawn are my own.

Finally, I would like to thank Dr Barbara Nowak for supervising this thesis.

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CHAPTER 1

GENERAL INTRODUCTION

BACKGROUND

Despite the growing body of work on coastal and nearshore marine ecosystems in Australian waters there is only limited information offshore. Further, most of these studies deal with single species (*eg.* Davis *et al.* 1990) or at most species groups (*eg.* Tranter 1977, Griffiths 1979). One of the first attempts at studying an oceanic ecosystem in Australian waters was the study of warm-core eddies and their inhabitants in the Tasman Sea in the early 1980s. In that study detailed oceanographic measurements (Cresswell 1983) were linked to the distribution of midwater fish (Brandt 1981, Brandt 1983a), squid (Brandt 1983b, Wadley 1985), crustacea (*eg.* Griffiths and Brandt 1981, 1983, McWilliams and Phillip 1983, Tranter *et al.* 1983, Young and Anderson 1987, Young 1989) and primary productivity (Jeffrey and Hallegraeff 1980). Wadley (1985) provided a synthesis of the fauna and identified faunal provinces in relation to the Tasman Sea eddies. A further study by Griffiths and Wadley (1986) identified midwater communities that could be distinguished by the water mass from which they were sampled. Since then there have been only two studies of midwater communities, both of which were off Tasmania (Blaber 1984, Koslow *et al.* 1994 but see also Koslow 1997). There is yet to be a study, however, of the relationships between midwater communities from adjacent inshore and offshore waters and the oceanographic processes that affect them.

One of the major limitations to understanding the ecology of midwater fauna has been the lack of suitable sampling technologies. Perhaps a greater limitation, however, is the notion that because these animals have no immediate commercial value there is little need for closer examination. However, an increased understanding of marine ecosystems and the resulting trend to multi-disciplinary approaches in studying them is changing this view. With improving capture techniques and advances in oceanography and acoustics, as well as developments in satellite imagery, analysis of the distribution and abundance of the non-commercial species is becoming more feasible. There are also increasing data that suggest predictive models of fisheries need inputs from such sources to more accurately understand changes in catch rates (Lyne *et al.* 1997).

Part of the problem in understanding the factors that affect oceanic fauna is that much of the ocean, although structured vertically (usually by temperature), is

relatively featureless horizontally. However, when one water mass (or current) meets another quite different oceanic conditions can exist over short ^{Spatial} space scales, from kilometers to as little as metres (Cushing 1982). The boundaries or fronts between these water masses, identified usually by gradients in temperature and salinity, can also create unique environments separate to those surrounding them (Brandt and Wadley 1981). Further, where these water masses butt up against the coast further potential for differences in environment can exist (Olsen *et al.* 1994). Comparisons between these different environments then can lead to understanding of the physical and biological factors that determine the distribution and abundance of micronekton and zooplankton. Where these currents meet with either land or other water masses there is generally an increase in nutrients via upwelling (Olson *et al.* 1994). The enhanced production of these areas commonly results in areas with relatively high levels of potential prey (*eg.* Olson and Backus 1985). These prey in turn attract larger predatory fish which regularly lead to the establishment of fisheries (*eg.* Podesta *et al.* 1993). An understanding of what drives the spatial dynamics of these “feed” species (in a fisheries sense), therefore, can help our understanding of the factors leading to the aggregation of commercial fish species.

Boundary currents (Tomczak and Godfrey 1994) fulfil most of the above requirements as they are close to the coast and interact with other water masses. As such they are generally major sites of ocean productivity in the world’s oceans, and so it is not surprising that many fisheries are associated with them (*eg.* Fiedler and Barnard 1987). The strength and extent of these currents have both a seasonal and interannual component. The effect of season is driven largely by distance from the equator. Temperate latitudes, therefore, are more affected than are latitudes closer to the equator (Cushing 1982). Interannual differences are driven by more complex cycles such as those of the often-reported El nino cycle of 7 to 10 years (in the southern hemisphere the El nino southern oscillation) (Quin 1974). Evidence for even longer-term cycles — Harris *et al.* (1988) reported a 45 yr. cycle in the southern hemisphere — is mounting.

The main current along the eastern seaboard of Australia is the East Australia Current. This current begins as an offshoot of the Tasman front at ~ latitude 30°S just south of Cape Byron and flows southward, generally to the southern tip of Tasmania

where it meets colder subantarctic origin waters at the subtropical convergence (Fig. 1).

THE FISHERIES AND FAUNA OF EASTERN TASMANIA

The waters off eastern Tasmania are home to a number of pelagic fisheries, most notably those for the southern bluefin tuna (*Thunnus maccoyii*) offshore and jack mackerel (*Trachurus declivis*) on the shelf. There are also some important inshore fisheries such as that for abalone and rock lobster but these are beyond the scope of this study. The fishery for southern bluefin tuna is largely carried out by Japanese longliners that supply the lucrative sashimi market in Japan, although Australian trollers and longliners are increasing their involvement. The meat is highly prized and can fetch upwards of 100 \$AUS per Kg. An annual quota of 400 t off Tasmania is usually met within a couple of months, between May and July (Caton *et al.* 1995), although variation in the catch between years is significant (Lyne *et al.* 1997). Interannual variations in catch rate are even more pronounced in the jack mackerel fishery off eastern Tasmania which, for example, took 40,000 t in the 1986–87 season but only 2 years later the catch was down to 8,000 t (Williams and Pullen 1993). Some of these variations can be attributed to fishing intensity or management policies. However, changes in the strength and position of the main water masses can, as Harris *et al.* (1987) proposed, also affect catch rates. Therefore, understanding the influence of physical and biological processes on fluctuations in these fisheries may lead to better management practices.

Both fisheries overlap the convergence of two water bodies, the East Australia Current and waters of subantarctic origin, which, depending on their relative strengths can have a major effect on the regional oceanography and thus on the associated fauna (Harris *et al.* 1987). These currents meet close to the coast and as such also have the potential to influence the main shelf and shelf break ecosystems. Jack mackerel and southern bluefin tuna are perhaps the most noticeable, and certainly the most commercial pelagic fishes in the area. However, there are other (non-commercial) pelagic species that are also integral to the area. Of these, two stand out — krill and lanternfish. Krill (*Nyctiphanes australis*) is widespread around the Tasmanian coastline. It is largely restricted to the continental shelf where it is the main prey for most fish and bird species of the area. Its importance is underlined when we consider that it is the sole prey for jack mackerel over the shelf. The latter,

at times, has supported the largest finfish industry in Australia (Johannes and Young in press). Using data from Ritz and Hosie (1982) and Young *et al.* (1993) densities of up to 10 g.m^{-2} are possible outside of swarms. The other main species group is the lanternfish. Although restricted to a thin band over the continental slope in waters of between 300 and 500 m depth, summer populations of lanternfish (composed mainly of *Lampanyctodes hectoris*) reach densities of 390 g.m^{-2} (May and Blaber 1989). This number is extraordinarily high when we consider that global estimates of lanternfish are usually between 0.1 and 6.5 g.m^{-2} (Gjosaeter and Kawaguchi 1980).

BIOLOGICAL OCEANOGRAPHY OF EASTERN TASMANIA

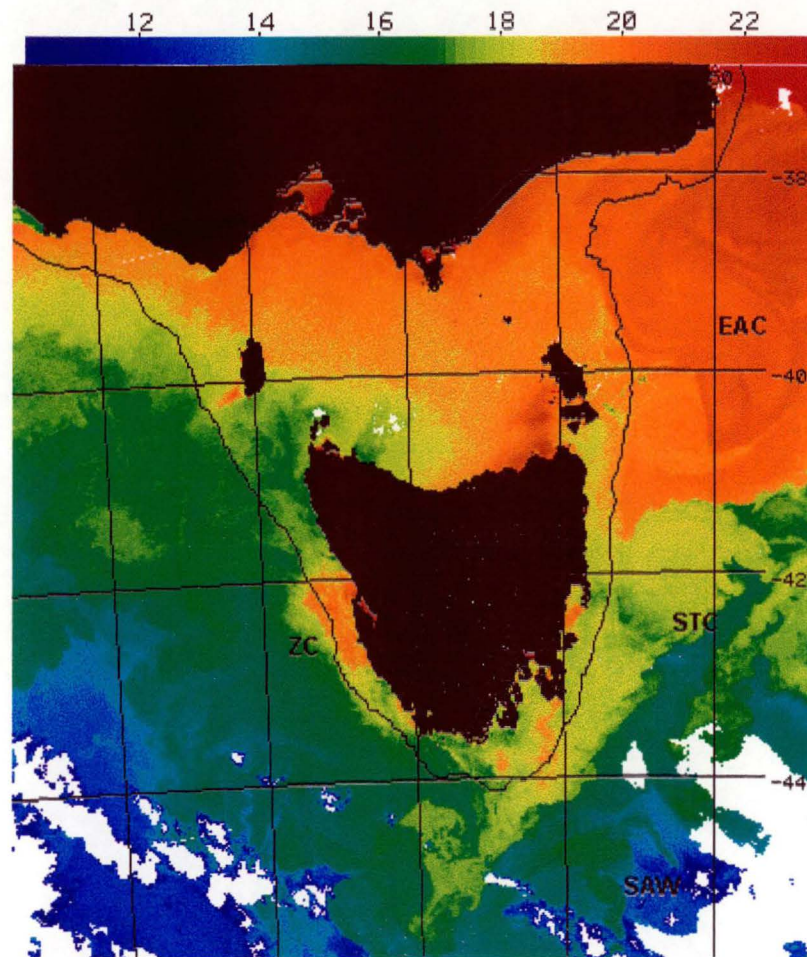
The Study Area

We first began the work on the shelf break off Maria Island in 1984. It soon became clear that this area, at the junction of East Australia Current water and subtropical convergence water was a dynamic area with respect to changes in the regional oceanography, and that it had a significant impact on the distribution and abundance of the associated fauna. For example, our initial exploratory trawls along the east coast of Tasmania had yielded small catches of myctophid fishes. Our knowledge of the slope demersal habitats had remained fairly static because there was limited trawlable seabed. On the advice of local fishermen (and to avoid the full brunt of the south westerlies) we started working over the area known as Darcy's Patch (Blaber *et al.* 1987). Almost immediately we started catching significant amounts of both midwater and demersal fishes (May and Blaber 1989). Later on, when we began studying southern bluefin tuna in the area we noted that the inshore fishery was restricted largely between Tasman Island on the southeast corner of Tasmania and Maria Island. Consequently, most of the studies I have described, particularly on the shelf and slope, have a narrow latitudinal range. It would appear that this area of the coast is relatively more productive than further north and it is also likely that the main reason for this is related to the interactions of the major water masses in the area (GP Harris, Pers. Comm.). I will discuss the influence of these water masses in the following chapters but it may be worthwhile to provide a brief summary here.

There are three main bodies of water which affect the east coast of Tasmania (Fig. 1). They are the waters of the subtropical convergence, the East Australia Current and the Zeehan Current. The former two generally separate approximately in the vicinity of Maria Island but this varies depending on the time of year and on year to year

a map
would have
been useful

variations. The Zeehan current, derived initially from Leeuwin Current water from western Australia is seasonal lasting from April to October (Cresswell *et al.* 1994).



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Figure 1: Satellite image showing the autumn position of the main water masses and currents off eastern Tasmania, Australia (EAC, East Australia Current; STC, Subtropical Convergence; SAW, Subantarctic Water; ZC, Zeehan Current). The cold tongue of northward flowing, southerly origin water usually found on the east coast continental shelf, has not yet begun.

In the ensuing papers I discuss the regional oceanography of the area. However, it should be noted that a central feature of the oceanography is that it is the convergence zone for East Australia Current water and waters of subantarctic origin (Wyrski 1960, Harris *et al.* 1987, Young *et al.* 1993). This zone, or subtropical convergence as it is known, has been the focus of a recent study (Clementson *et al.* in press) and its boundaries have been extended beyond that reported here, although I reported the change in definition in an addendum to Chapter 3. Basically, the subtropical convergence is now defined as the surfacing of the 34.9 PPT isohaline

and can extend as far south as 47°S. Off South Africa and New Zealand this zone is far more abrupt than off Tasmania where it can extend over a couple of degrees of latitude, indicating that physical gradients (fronts) in the area are more gradual. Hence, what I refer to as subantarctic water will soon be regarded as waters of the Subtropical Convergence. Nevertheless, such a change in nomenclature does not change the conclusion that the front off eastern Tasmania is the result of the meeting of East Australia Current water with waters of subantarctic origin.

Seasonal and Interannual Changes

In the Australian summer the East Australia Current extends southward, bringing warm, generally nutrient poor water down the east coast of Tasmania where it dissipates, either through the formation of eddies or via mixing with convergence waters. At this time the East Australia Current is usually stratified, through lack of wind mixing, with little added production. With the onset of autumn the strength of the prevailing westerlies increases, forcing waters of southern origin northward inhibiting the flow of the East Australia Current. The depth of the mixed layer increases bringing nutrients into the surface waters where they are fixed by algae generating the autumn bloom. There is another bloom in spring resulting from the equinoctial westerlies that are prevalent at the time (Harris *et al.* 1987).

Overriding the seasonal pattern are interannual climatic variations that correlate with the El Nino Southern Oscillation cycle. This cycle can vary from 4 to 7 years (Harris 1988). More recently, Pook (1992) has shown a strong correspondence also with the strength of zonal westerlies to the south and southwest. The overriding effect of these physical changes determines the relative importance of northern or southern water on the regional oceanography.

Inshore/Offshore Processes

Although not separate from the general circulation patterns of the area the movement of waters alongshore and between inshore and offshore around Tasmania has been less clearly studied. In fact a study has just begun to examine these patterns (Cresswell 1997). Nevertheless, drifter buoys over the past few years have shown that there is the capacity for both inshore and offshore movement of currents in the area (Cresswell *et al.* 1994). Bruce *et al.* (in prep.) proposed an inshore/offshore

circulation pattern that influences the recruitment patterns of at least jackass morwong (*Nemadactylus macropterus*) and southern rock lobster (*Jasus edwardsii*).

AIMS AND STRUCTURE OF THE THESIS

The overall goals of this research are twofold. Firstly, to develop an understanding of the physical and biological processes affecting the midwater zooplankton and fish community, and their relationship with coastal waters, off eastern Tasmania.

Secondly, I aimed to develop an understanding of the links between these groups and top predators such as southern bluefin tuna.

In the series of papers which make up this thesis I have examined the make up of the pelagic fauna off eastern Tasmania in parts (individual species) and the interactions between these parts to lead to an understanding of the whole (community). On the one hand I have examined individual species of zooplankton (Chapters 2 and 8) and micronekton (Chapters 5, 6, 7 and 9). I have then attempted to take a broader view of overall community processes (Chapters 3 and 4) and the links not only with the regional oceanography but also between the inshore and offshore region.

A number of the papers in this study deal with the feeding ecology of the resident fishes, from their larvae (of jack mackerel, Chapter 8) through micronektonic fish (Chapter 7) to mid order (Chapter 2 deals with feeding ecology of jack mackerel) and top order predators such as southern bluefin tuna (Chapter 9). This has helped to link the movements of the fauna and the processes that affect them. It also enabled me to develop an understanding of some of the major trophic pathways of the region. The growth and reproduction studies of individual midwater fishes (Chapters 5 and 6) are examples of the strong seasonal cycles evident off eastern Tasmania. Finally, a number of the studies were based on three year sampling periods (Chapters 2, 3, 4, 8 and 9) enabling interpretations of interannual cycles in the data.

Apart from Chapter 10 all the work is in the form of published papers. By the very nature of the work it has required a great deal of team-work and collaboration in both the field work and analysis of samples. However, the research plans, implementation (I was cruise leader on all the *Southern Surveyor* and *Scottsman* cruises and three of the six *Soela* cruises — Alan Jordan led the *Challenger* cruises) and the conclusions are my own and any individual contributions have been acknowledged.

The papers that make up this thesis follow the three basic questions outlined by McGowan (1971) in studying planktonic communities. These are:

1. What species are present?
2. What are the main patterns of distribution and abundance?
3. What maintains the shape of the patterns?

The identification of zooplankton species on the shelf has been documented (Nyan Taw 1975). In this study I focused on the krill as they form the greatest biomass of the zooplankton in these waters. Over the slope, although I identified the midwater component of the fish sampled, that paper was published separately (May and Blaber 1987). My work concentrated on the ecology of the main midwater fish species of that mix. Offshore, I was able to take a broader view, examining species composition, as well as their patterns of distribution and biomass.

To answer the third question on what maintains the shape of these patterns it was necessary to study not only physical factors but biotic ones as well. I have taken the view that “bottom up” (Harris and Griffiths 1987) processes were important determinants of the patterns we were observing. That is, the availability of zooplankton (feed) determines the presence, or absence, of larger predators. The reverse or “top down” approach (Carpenter and Kitchell 1987) believes that predators control the levels of lower orders in a “trophic cascade”, as identified in some freshwater lakes. Either position is difficult to prove in such an open water system. However, my perception of this debate relates to the idea of density-dependence. In my experience (and only for larval fish) the “top down” scenario would be more likely in a tropical system rather than the temperate one where this study was based (for a comparison see Young and Davis 1990 and Chapter 8). Fortunately, Harris and his co-workers’ position led to studies of the primary productivity of Tasmanian waters, data that I was able to draw upon throughout this study (see Harris *et al.* 1987).

The papers in this thesis have been written over 10 years. Therefore, I thought it would be appropriate to detail some of the major procedural and technological advances that I have been associated with during the course of the study, and to discuss where some of these developments can lead. For example, Chapters 3 and 4

are, to my knowledge, the first published accounts of the vertical distributions of midwater fishes in Australian waters. This was possible through the use (and development by CSIRO) of an opening-closing codend attached to a midwater trawl.

PART A

DISTRIBUTIONAL STUDIES

CHAPTER 2

**Seasonal and interannual variations in krill (*Nyctiphanes australis*)
stocks and their relationship to the fishery for jack mackerel
(*Trachurus declivis*) off eastern Tasmania, Australia.**

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Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia

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Abstract. *Nyctiphanes australis* was collected from the east coast of Tasmania between January 1989 and April 1991. Density and biomass were significantly higher in autumn than in any other season. The population was dominated by juveniles, except in autumn and spring 1990 when there was a significant increase in the proportion of adults. Our data indicated that *N. australis* does not regularly migrate vertically and that it forms aggregations of particular size classes which vary both temporally and spatially. Stomach fullness in *Trachurus declivis*, a major predator of *N. australis*, rose to a peak in autumn when *N. australis* stocks and the monthly catches by the fishery for *T. declivis* were at their highest. The stomachs of *T. declivis* were also dominated by adult size classes during this period. The virtual absence of *N. australis* in 1989 and the subsequent failure of the *T. declivis* fishery in that year underline the interrelationship between these two species. We suggest that this was the result of an influx of subtropical northern waters low in nutrients onto the shelf, which corresponded with a major La Niña “cold event” at that time.

Introduction

Seasonal and interannual variations in the movements of water masses can have profound effects on the structure of marine communities (Cushing 1982). Lower productivity and subsequent changes in the structure of the zooplankton community appear to be a common response to the intrusion of warm water into cooler regions and a decrease in wind-mixing. This happens particularly during El Niño years (Fulton and LeBrasseur 1985, McGowan 1985, Sambrotto 1985, Smith 1985).

Off eastern Tasmania, seasonal and interannual levels of productivity are determined by the interaction of warm, nutrient-poor East Australian Current (EAC) water and cool, nutrient-rich subantarctic water (Harris

et al. 1987, 1991). During the summer of 1988/1989, the shelf waters of south-eastern Tasmania experienced an increased influx of subtropical waters and an associated decrease in production, apparently related to the large El Niño/Southern Oscillation (ENSO), or La Niña “cold event” of 1988 (Harris et al. 1991). They found that this event was accompanied by the loss of large zooplankters, particularly the euphausiid *Nyctiphanes australis*, from the system.

Nyctiphanes australis is a major component of the zooplankton community in coastal waters of south-eastern Tasmania (Nyan Taw and Ritz 1979, Blackburn 1980, Ritz and Hosie 1982). Ritz and Hosie found this species in high densities throughout the year in Storm Bay, although seasonal differences were apparent. *N. australis* is the main prey of many coastal bird and fish species in Tasmanian waters (O’Brien 1988), including *Trachurus declivis*, which feeds on it almost exclusively in surface waters during summer and autumn (Webb 1976). A rapidly developing purse-seine fishery for *T. declivis* has operated near Maria Island on the east coast of Tasmania since 1985, with annual landings increasing to 39 750 tonnes by 1987 (Williams et al. 1987). The Tasmanian fishery depends upon the surface schools of *T. declivis* that feed on *N. australis* swarms. Consequently, any change in the density of *N. australis* may have a direct effect on *T. declivis* schooling behaviour and the amount of fish available to the commercial fleet (Williams and Pullen 1993).

This paper aims to (1) examine variations in the density and biomass of *Nyctiphanes australis* in relation to seasonal and interannual variations in the physical oceanography of eastern Tasmania, and (2) assess whether these variations have any impact on the local *Trachurus declivis* fishery.

Materials and methods

Nyctiphanes australis was sampled on both fine (<1 km) and coarse (1 to 10 km) scales in the vicinity of Maria Island, eastern Tasmania (Fig. 1), between January 1989 and April 1991. Samples were col-

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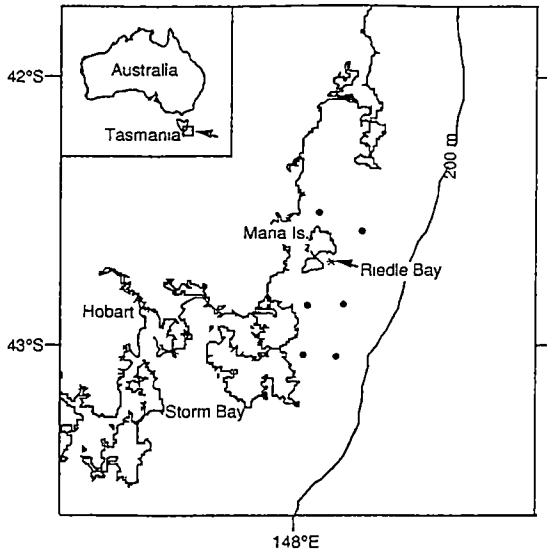


Fig. 1. Location of sampling stations (●) for *Nyctiphanes australis* around eastern Tasmania

Table 1. Sampling times, areas and number of samples collected off eastern Tasmania. –: no samples. Total $n=237$. See Fig. 1 for positions of Riedle Bay and coarse-scale samples

Month	Riedle Bay			Coarse-scale sampling		
	1989	1990	1991	1989	1990	1991
Early Jan.	–	1	8	6	6	6
Late Jan.	–	–	–	6	6	6
Feb.	–	10	–	6	6	6
Mar.	–	15	–	–	6	6
Apr.	–	10	–	6	–	6
May	–	10	–	–	–	–
June	–	16	–	–	–	–
July	–	5	–	–	–	–
Aug.	–	12	–	–	–	–
Sep.	–	14	–	–	–	–
Oct.	6	17	–	–	–	–
Nov.	10	9	–	–	–	–
Dec.	3	13	–	–	–	–
Total	19	132	8	24	24	30

lected from a site off Riedle Bay at approximately monthly intervals from October 1989 to January 1991 to examine variations in the density and population structure of *N. australis*. To examine variability in the density and biomass of *N. australis* between years, sampling was also done at a coarse scale from a grid of stations inshore and on the continental shelf in the vicinity of Maria Island (Fig. 1) at fortnightly or monthly intervals during the fishing season of January to April in 1989, 1990 and 1991 (Table 1; see also Young and Davis 1992).

At Riedle Bay, plankton was collected from replicate tows during the day and night along the 80 m depth contour. Surface tows and oblique tows to ~40 m depth were made either simultaneously or consecutively. Ring nets equivalent to one side of an Ocean Instruments 70 cm bongo net were used. Nets were cylindrical-conical, with a mesh aperture of 500 μ m and an open area ratio of 5:1. All nets were dyed blue to reduce net avoidance (LeBrasseur et al. 1967). A General Oceanics mechanical flowmeter (calibrated over a measured mile in the Derwent River, Tasmania) was hung inside each net, and used to record the volume of water sampled. All tows

were made at ~3 knots for ~10 to 20 min. Maximum depth was measured by a diver's depth gauge with a maximum-depth indicator.

For the 11 tows when a flowmeter was not used, the volume filtered was estimated from the regression of flowmeter count versus tow time (flow count = $3045 \times \text{tow time (min)} + 6477$, $r^2 = 0.55$, $n=123$). Samples were preserved in 5% seawater-formalin buffered with sodium acetate. Temperature ($\pm 0.01^\circ\text{C}$) and salinity ($\pm 0.01\text{‰}$) data were obtained from the monthly records of the CSIRO coastal monitoring station off Maria Island ($42^\circ 36'\text{S}$; $148^\circ 16'\text{E}$) (Harris et al. 1987) from depths of 10 and 50 m. Data collected from 10 m depth were considered to be indicative of surface waters and will be referred to as such in the text.

Coarse-scale sampling consisted of single tows at each of the six stations (Fig. 1). Bongo nets with a mouth opening of 45 cm, 500 μ m-mesh netting and an open-area ratio of 5:1 were used. All sampling was completed in daylight hours (06.00 to 20.00 hrs). Each sample consisted of an oblique tow to a maximum depth of 100 m (bottom depth permitting) at a tow speed of ~3 knots. At each station the net was sent to the required depth quickly, held there for 1 to 2 min and then retrieved on an oblique path. The volume of water filtered was estimated with flowmeters as in the fine-scale study. Temperature and depth were recorded with a temperature-depth probe attached below the net. Surface temperatures were recorded directly from the on-board temperature recorder ($\pm 0.01^\circ\text{C}$). Samples from one side of the bongo were fixed in 95% ethanol, and from the other side in buffered 5% seawater-formalin.

In the laboratory, samples of *Nyctiphanes australis* were split to a manageable size (mean $\pm 95\%$ confidence interval of 157 ± 19.7 individuals per subsample) with a Folsom splitter, and the subsample was counted. Each individual was measured from the tip of the rostrum to the end of the telson (± 0.1 mm) (Standard 1 of Mauchline 1980) and grouped into four size classes [≤ 5.0 mm (I); 5.1 to 7.5 mm (II); 7.6 to 11.0 mm (III); ≥ 11.1 mm (IV)]. These size classes corresponded approximately to calyptopsis and furcilia stages (I), post-larvae (II), adolescents (III) and adults (IV) (Sheard 1953, Hosie 1982). Formalin-preserved specimens from each size class were measured, oven-dried at 60°C for ~4 h and weighed (± 0.005 mg). There was no change in the relationship between length and weight of *N. australis* with season (ANCOVA, $p > 0.10$).

Trachurus declivis were collected from January to June 1990 from the commercial fishery that operates around Maria Island during this time (Williams and Pullen 1993). Their stomachs were removed and weighed (± 0.1 g). For each fish examined, length to caudal fork (LCF, mm), total wet weight (W , ± 0.1 g) and stomach weight (S , ± 0.1 gm) were recorded. Stomach fullness was presented as S/W , 100%. Stomach contents were dominated by *Nyctiphanes australis*, although amphipods (*Themisto gaudichaudii*), calanoids, crab zoea and fish larvae were also present, but as these taxa represented $< 1\%$ of the diet (C. Bobbi unpublished data), they were not considered further. *N. australis* from each stomach were suspended in water, split to a manageable number (see preceding paragraph) and grouped into their respective size classes.

Data analysis

Total sample size was estimated by the formula: count $\times 2^n$, where n is the number of splits (Omori and Ikeda 1984). The biomass (B) of *Nyctiphanes australis* in each sample was estimated from the equation:

$$B = \sum_{s=1}^4 P_s \cdot N_t \cdot W_s, \quad (1)$$

where P_s is the numerical proportion of a size class in the sample, N_t the total number in the sample, W_s is the mean dry weight of the size class (Table 2), and s is the number of size classes. The density of *N. australis* was calculated by dividing the estimated number caught by the volume of water filtered. Similarly, biomass was calculated by dividing total estimated biomass by the volume of water filtered.

Table 2. *Nyctiphanes australis*. Mean length (L) and mean dry wt of the different size classes

Size class (mm)	\bar{x} L (mm)	\bar{x} wt (mg)	(n)
I (<5.0)	2.83	0.093	(22)
II (5.01–7.5)	6.15	0.267	(29)
III (7.51–11.0)	8.84	0.747	(51)
IV (11.01+)	13.38	2.458	(59)

Comparisons of density and biomass between seasons, depths (surface/oblique) and times of day (day/night) were made on data from the fine-scale study by multiway ANOVA. Empty cells in the first two seasons (sampling initially consisted of oblique tows during the day) meant that this analysis was eventually restricted to four seasons (autumn 1990 to summer 1991). Since the distribution of density and biomass values of samples was skewed, the data were transformed to best approximate the assumptions of normality and equal variance among the residuals (Zar 1984). Therefore, density values were transformed to $\ln(\text{density} + 1)$ and biomass values were transformed to $(\text{biomass} + 1)^{-1}$, as these transformations gave the most even distribution of residuals versus fitted values.

We examined changes in the proportions of individual size classes between seasons by contingency tables with loglinear analysis (Dobson 1983), based on the assumption that the number of *Nyctiphanes australis* in each size class at a given station followed a multinomial distribution. Stations were divided into season [spring 1989 to summer 1990/1991 ($n=6$)], time of day (day or night), and depth (surface or oblique). Size Classes III and IV were pooled to obtain sufficient numbers in this class. Initial analyses showed significantly greater variation than would be expected by random variability (e.g. for day oblique tows within a season, chi-square=6894, $df=142$, $p<0.0001$). A close inspection of the data revealed that the extra variability was due to single samples (patches) being dominated by a particular size category. Therefore, the usual chi-square tests were replaced by *F*-tests, with the chi-square statistic allowing for the extra-multinomial variation in the denominator.

In both ANOVAs and the loglinear contingency-table analyses, comparisons of individual means or proportions were made only when the main effects were significant, following Fisher's protected least-significant-difference procedure (Snedecor and Cochran 1980).

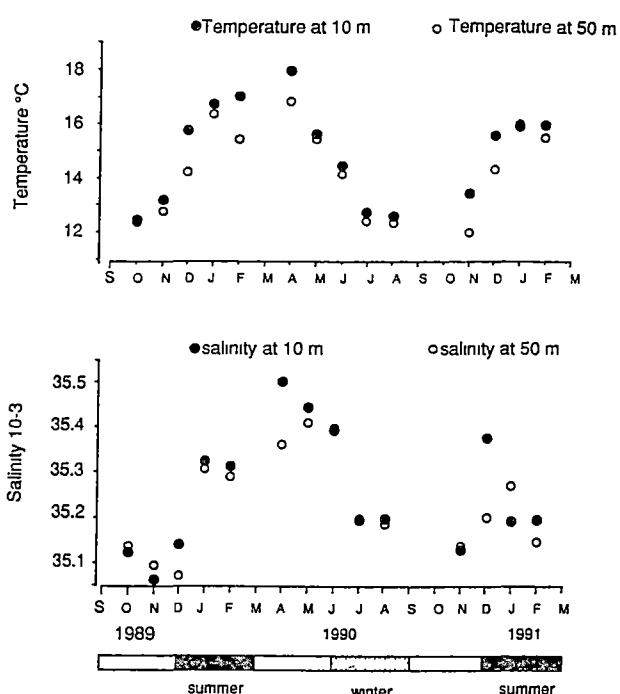
Interannual differences in *Nyctiphanes australis* biomass were compared by ANOVA on the coarse-scale data. Selection for prey size was examined using Pearre's C-index (Eq. 3, p. 915 in Pearre 1982). Each size class of *N. australis* was treated as an individual taxon and its proportion in the environment was compared with that in the stomachs of individual *Trachurus declivis*.

Results

Physical oceanography

Fine-scale

Surface temperatures increased from 12°C in winter to 17°C in late summer and early autumn in 1990 (Fig. 2) due to seasonal warming and the intrusion of subtropical EAC water onto the shelf. Salinity increased over this period from 35.1 to 35.5‰. The 17°C, 35.5‰ S signature is characteristic of EAC water (see Fig. 1 in Harris et al. 1987). The intrusion of this water onto the shelf in summer–autumn 1990 resulted in stratification. The water column was well mixed in late autumn to late spring 1990

**Fig. 2.** Monthly water temperatures and salinity (‰) at depths of 10 and 50 m at Maria Island monitoring station between October 1989 and February 1991

and stratified in summer, when a short pulse of high-temperature, high-salinity EAC water intruded onto the shelf (Fig. 2). However, unlike the previous year, the pulse did not persist in the summer of 1991.

Coarse-scale

Sea-surface temperatures for the summer and autumn of 1989, 1990 and 1991 reflected seasonal warming and the changing influence of warmer northerly and cooler southerly water on the region (Fig. 3). In general, 1989 may be characterised as the warmest year of the three-year study, 1991 the coolest, and 1990 as intermediate. However, even during the “coolest” year of 1991, temperatures over 17°C were recorded in parts of the study area.

In early January 1989, surface waters were between 16.0°C and 17.0°C (Fig. 3). By late January, warmer water of northerly origin, previously identified as EAC water, began to spill across the shelf, dominating the area by late February. By April, warm water still dominated the area although some cooling was apparent. In early January 1990, most water in the study area was between 16.0°C and 16.5°C. By February, warmer northerly water had moved into the area, raising temperatures to around 17.5°C. The advance of cooler southerly waters in March resulted in the partial retreat of warm water.

Temperatures in the summer of 1991 were consistently cooler than previous years, reflecting the reduced influence of warmer northerly water (Fig. 3). By late February, waters were as much as 3.2°C cooler than for the

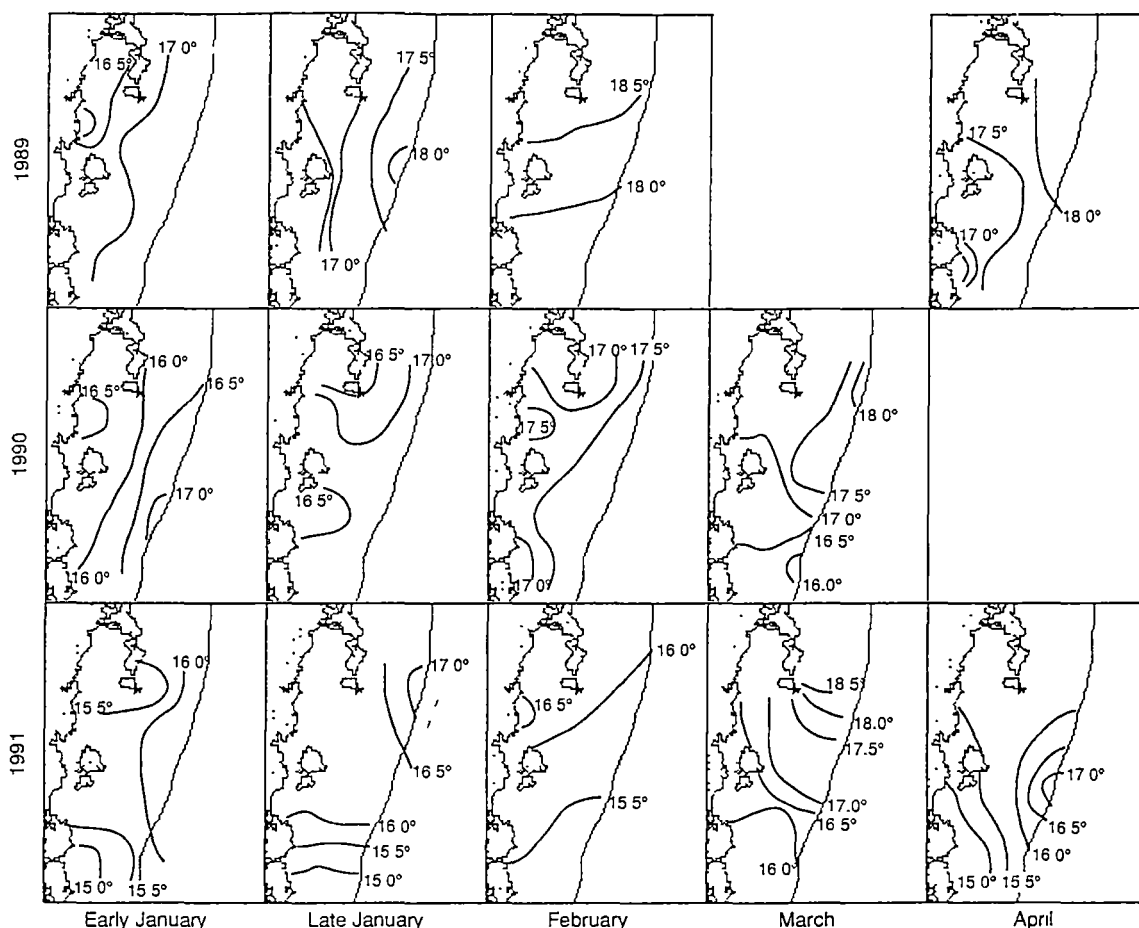


Fig. 3. Distribution of sea-surface temperatures ($^{\circ}\text{C}$) in shelf waters of eastern Tasmania during summer and autumn of 1989, 1990 and 1991

same period in 1989. However, warmer water advanced from the north in March, with temperatures varying by 1.8°C between the northerly and southerly transects. Rapid cooling had taken place by April as cooler water pushed up from the south.

Considerable interannual variability in thermal stratification is apparent in the three years of the study (Fig. 4). The strong thermocline that existed in the summer of 1989 weakened during autumn, although there was still a temperature gradient of $\sim 3^{\circ}\text{C}$ between surface and bottom waters. In January 1990, the thermocline was both deep ($\sim 55\text{ m}$) and distinct. In the following months, the mixed layer had become shallower and the thermocline had become weaker. During late summer and autumn in 1991, the water column was well mixed with no sign of thermal stratification. However, the March profile from the northern transect shows the presence of a strong thermocline, resulting from the advance of a shallow layer of warm water from the north (Fig. 4).

Seasonal changes in density and population structure

In the fine-scale study, a total of 159 tows were made, spread over six seasons between October 1989 and January 1991 (Table 1: Riedle Bay). The density of *Nyctiphanes*

Table 3. *Nyctiphanes australis*. Three-way ANOVA of $\ln(\text{density} + 1)$ and $(\text{biomass} + 1)^{-1}$ as a function of season, depth and time of day

Source	df	Density		Biomass	
		F		F	p
Season (A)	3	3.38	0.021	3.26	0.024
Depth (B)	1	1.1	0.297	0.85	0.358
Diel (C)	1	2.7	0.102	3.36	0.070
A \times B	3	1.54	0.207	1.15	0.332
A \times C	3	0.62	0.607	1.01	0.392
B \times C	1	0.82	0.368	0.80	0.372
A \times B \times C	3	2.31	0.080	1.51	0.215
Error	113				
Total	128				

australis in individual samples ranged from 0 to 358 individuals m^{-3} (biomass 0 to 51 mg m^{-3}). In general, *N. australis* density and biomass increased to a maximum in autumn 1990, declined through winter, and increased gradually in spring (Fig. 5).

Nyctiphanes australis density differed significantly between seasons but not between depth or time of day. No significant interaction was found between season, depth

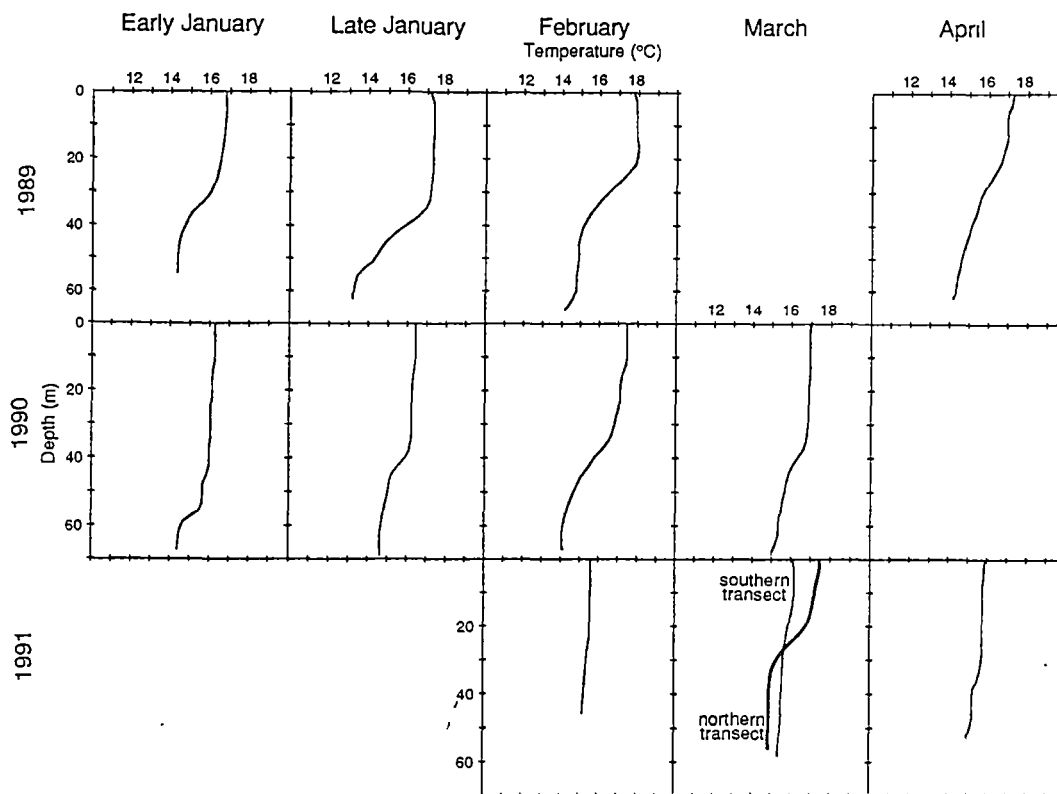


Fig. 4. Vertical temperature profiles at midshelf station immediately south of Maria Island during summer and autumn of 1989, 1990 and 1991. For March 1991, profile from midshelf station north of Maria Island is also presented (heavy line)

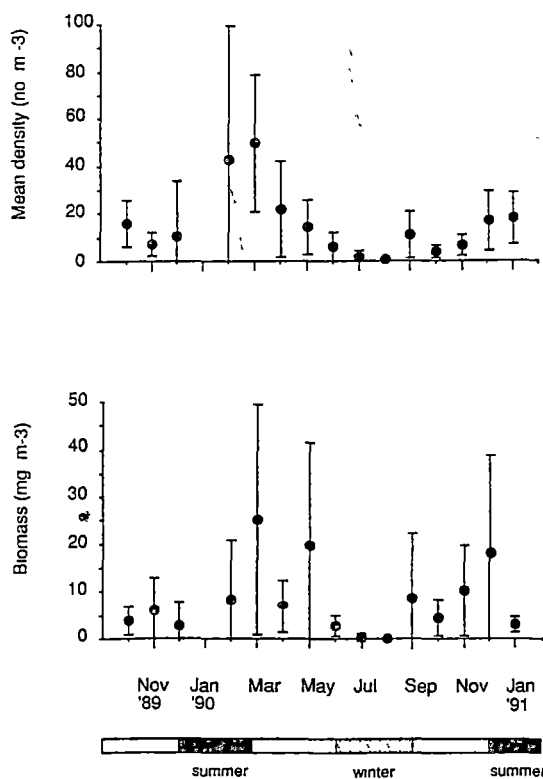


Fig. 5. *Nyctiphanes australis*. Monthly density and biomass at Riedle Bay (means \pm 95% confidence limits)

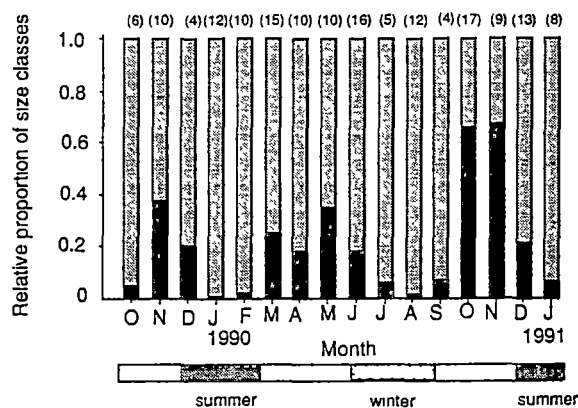


Fig. 6. *Nyctiphanes australis*. Relative proportions of size classes between months at Riedle Bay. Stippled portions represent Size Classes I and II combined, black portions represent Size Classes III and IV combined. Nos. in parentheses on top abscissa indicate number of samples

and time of day (Table 3), indicating that seasonal effects were not significantly different at different depths or times of day. *N. australis* density was highest during autumn 1990. There was a significant difference in biomass between seasons but not with depth, time of day or their interactions (Table 3). Biomass was also highest in autumn 1990.

The size-class structure of *Nyctiphanes australis* was dominated by Stage I and II individuals throughout the

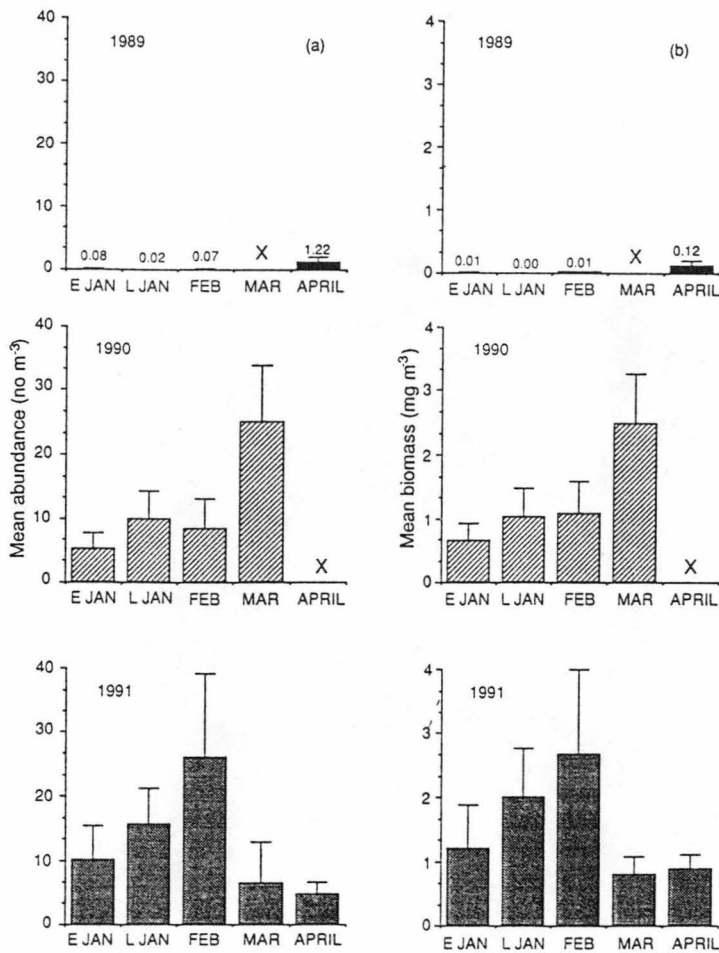


Fig. 7. *Nyctiphanes australis*. Interannual changes in density and biomass recorded during coarse-scale sampling off eastern Tasmania in 1989, 1990 and 1991 (means \pm 1 SE; $n=6$ for all samples). E JAN, L JAN: early and late January respectively; X: no sampling

study period, indicating continuous reproduction (Fig. 6). However, pulses of Stage III and IV *N. australis* were noted in late spring in 1989 and 1990 and also in autumn 1990 (Fig. 6). Closer examination revealed that there was significant variation in the size distributions of *N. australis* between seasons ($F=5.85$; $df=10,300$, $p<0.001$), and between different depths and times ($F=4.85$, $df=6,300$, $p<0.001$), but no interaction between season, depth or time of day ($F=0.52$, $df=24,276$, $p>0.05$). Because of unequal replication and for ease of interpretation, different depth and time combinations were analysed separately for seasonal effects.

For day oblique tows, size distributions varied significantly between seasons ($F=6.82$, $df=10,166$, $p<0.001$). Specifically, summer 1989–1990 and spring 1990 differed from the other four seasons ($F=15.24$, $df=4, 172$, $p<0.001$). In summer 1989/1990, large-sized (Size Classes III and IV) *Nyctiphanes australis* were almost absent from the samples (Size Classes III and IV comprised only 2% of the total by numbers), whereas in spring 1990 large-sized *N. australis* comprised nearly half the population (43% of total). The relative proportions of size classes in the remaining seasons were not significantly different from each other ($F=1.16$, $df=6, 166$, $p>0.05$). Size distributions of *N. australis* from surface tows during the

day were not significantly different between seasons ($F=1.92$, $df=8, 82$, $p>0.05$).

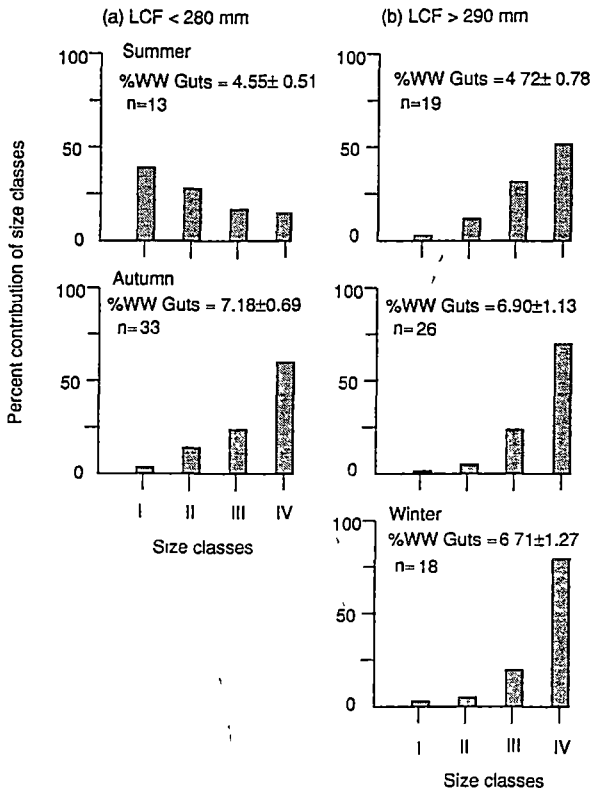
At night there was no significant difference in size distributions between surface and oblique tows ($F=0.17$, $df=6, 52$, $p>0.05$). We therefore combined data from both sets of tows and found that at night there was a significant difference in size distributions between seasons ($F=3.30$, $df=10, 60$, $p>0.01$). Larger-sized *Nyctiphanes australis* dominated the night samples in spring 1990, reflecting the pattern seen in the daytime samples. No night samples were taken in summer 1990.

Interannual differences

Nyctiphanes australis densities varied significantly and dramatically between the three years in which samples were taken. In 1989, density was significantly lower (mean of 0.38 individuals m^{-3}) than in 1990 (12.25 m^{-3}) and 1991 (12.79 m^{-3}) (ANOVA, $F=5.2$, $df=72$, $p=0.008$) (Fig. 7). Similarly, *N. australis* biomass was two orders of magnitude lower in 1989 (0.04 mg m^{-3}) than in 1990 (1.32 mg m^{-3}) and 1991 (1.53 mg m^{-3}) (ANOVA, $F=7.2$, $df=72$, $p=0.001$). In each year, the density and biomass increased through summer and au-

Table 4. *Trachurus declivis*. Pearre's index of prey selectivity for fish of 190 to 280 mm (<280 mm) and 290 to 380 mm (>290 mm) length to caudal fork preying on different size categories of *Nycti-**phanes australis* during 1990 fishing season. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Index ranges from -1 (negative selection) to +1 (positive selection) (n): number of fish examined

Month (n)	<280 mm				>290 mm			
	I	II	III	IV	I	II	III	IV
Jan. (10)	-0.22 **	+0.16 *	+0.06	+0.10	-	-	-	-
Feb. (22)	-0.65 ***	+0.01	+0.31 ***	+0.25 ***	-0.68 ***	-0.01	+0.18 *	+0.33 ***
Mar. (7)	-	-	-	-	-0.22 **	-0.09	+0.01	+0.31 ***
Apr. (14)	-0.34 ***	+0.04	+0.03	+0.06	-0.47 ***	+0.01	+0.08	+0.22 **
May (44)	-0.12	-0.12	+0.01	+0.18 *	-0.14	-0.14 *	+0.01	+0.23 ***
June (18)	-	-	-	-	-0.32 ***	-0.17 *	+0.03	+0.50 ***

**Fig. 8.** *Nyctiphanes australis*. Changes in relative proportions of individual size classes in stomachs of two size classes (length to caudal fork <280 mm and >280 mm) of *Trachurus declivis* in 1990. % WW Guts: ratio (%) of wet weight of stomach to total fish wet weight

turn. The 1990 data from the fine- and coarse-scale studies were compared. Although the latter displayed a relatively lower density and biomass (most probably due to the use of a net with a smaller mouth opening), both studies showed a trend for density and biomass to increase over summer and autumn (cf. Figs. 5 and 7).

Stomach contents of *Trachurus declivis*

The stomach contents of 115 *Trachurus declivis* sampled between January and June 1990 were examined. Fish

ranged in size from 190 to 370 mm LCF and were comprised of two size classes: one from 190 to 280 mm LCF and the other from 290 to 370 mm LCF. The ratio (%) of stomach wet weight to total fish weight ranged from 4.66 to 7.04% in the fish examined. This percentage was significantly lower in January 1990 (summer) than in the following autumn and winter (ANOVA, $F=9.0$, $df=102$, $p=0.0001$; Fig. 8), suggesting increased feeding in these latter months. Their diet was dominated almost entirely by *Nyctiphanes australis*. However, differences were noted in the relative proportions of the different size classes at different times of the fishing season.

The proportion of Size Classes I and II of *Nyctiphanes australis* in the stomachs of *Trachurus declivis* was significantly different between months, and was higher at the beginning of the fishing season than at the end (ANOVA, $F=237.0$, $df=114$, $p=0.0001$; Fig. 8). Conversely, the proportion of adult *N. australis* in the samples of larger-sized *T. declivis* increased as the season progressed (ANOVA, $F=127.0$, $df=114$, $p=0.0001$) (cf. Fig. 6). Comparison of the relative proportions of size classes in the guts of *T. declivis* with those present in the plankton showed that there was generally negative selection for the smaller size classes and positive selection for adults throughout the study period (Table 4).

Discussion

Vertical migration

Species of *Nyctiphanes* are thought to migrate vertically (Sheard 1953, Blackburn 1980, Williams and Fragopoulou 1985). Blackburn (1980) proposed that *N. australis* descends to the bottom during the day and migrates to the surface at night off eastern Australia. However, we found no evidence of a consistent pattern of vertical migration. In fact, the densities in many of our day surface-hauls were equivalent to or greater than those in the accompanying deep haul. Similarly, O'Brien (1988) reported swarms during daytime off eastern Tasmania. Diurnal vertical migration was not found for *N. simplex* off California (Fiedler and Bernard 1987), where swarms were reported at the surface during daytime. Possibly Blackburn's (1980) study was biased by the sampling strategy, which was based largely on upward vertical hauls. Hov-

erkamp (1989) found that euphausiid catches from downward hauls were about nine times greater than those from upward hauls, suggesting that euphausiids are more capable of avoiding upward hauls. Our conclusions are limited by the use of open nets. Nevertheless, by using nets towed simultaneously in surface and deep waters, we are confident that we could detect gross vertical distributional trends. In the present study we found that neither the depth nor the time of day from which samples were taken significantly affected the estimates of *N. australis* density and biomass in the region.

Seasonal and interannual cycles in density

Our results provide evidence that the density and biomass of *Nyctiphanes australis* undergoes seasonal and interannual cycles off eastern Tasmania. The seasonal cycle appears to be driven by a series of events. In summer, annual intrusions of oligotrophic subtropical (EAC) water flood the shelf, creating an environment low in both nutrients and phytoplankton, the major food source of *N. australis* (Ritz et al. 1990). With the retreat of this nutrient-poor water and seasonal cooling in autumn, nutrients are once more available to drive production (Harris et al. 1987), hence the increase in *N. australis* stocks and their subsequent availability to *Trachurus declivis*. The reasons for the decrease in *N. australis* stocks over winter, found in this and a previous study by Ritz and Hosie (1982), are less clear. It may be, as Blackburn (1980) suggested, that some members of the population overwinters by descending to the seabed where they would not be detected by plankton tows. That stomachs of bottom-dwelling tiger flathead (*Platycephalus richardsoni*) sampled during winter in the same area were filled with *N. australis* supports this view (Hosie 1982). Other factors, such as predation during autumn, may also reduce stocks surviving through to winter. The increase in numbers after winter appears to be a function of the spring phytoplankton bloom at that time (Harris et al. 1987). The increase in the relative proportion of adults compared to smaller size classes in both the spring and autumn blooms is noteworthy. Generally our samples were dominated by calyptopis and furcilia stages through the year. However, the proportion of adults was significantly higher in both autumn and spring 1990. If adult stocks do descend to the seabed during periods of low food supply, then the onset of the algal blooms (or some correlate) might trigger the adults to rise into mid- and surface-waters to feed.

Overlying these seasonal cycles in density of *Nyctiphanes australis* are interannual variations which we found to be at least an order of magnitude in difference. These differences are presumably directly related to interannual variations in the regional oceanography. Harris et al. (1987) proposed that the relative importance of the two major water masses – warm, stratified, nutrient-poor EAC water and cool, well-mixed, nutrient-rich water of subantarctic origin – from year to year is determined by a combination of the local westerly wind stress and large-scale oceanographic circulations often associated with ENSO events. The boundary that separates these two

water masses is defined as the subtropical convergence (STC), which in summer often lies in the vicinity of Maria Island (Harris et al. 1987). The position of the STC, however, shows considerable interannual variability and has been coupled with interannual variations in westerly winds (Harris et al. 1988). The Maria Island area experienced warm water temperatures and strong thermal stratification during the entire summer and autumn of 1989, resulting from a reduction in the westerly wind stress and an increasing influence of subtropical EAC water. This event has been linked to the major La Niña “cold event” in the southern hemisphere (Harris et al. 1991).

The interannual variability in the regional oceanography of south-eastern Tasmanian waters has profound effects on the nutrient cycling and structure of the food chain (Harris et al. 1991). In the summer of 1988/1989, Harris et al. (1991) found that the increase in subtropical influence in Storm Bay, ~55 km south of the study area, resulted in a decrease in local productivity, which led to the disappearance of the large zooplankters, principally *Nyctiphanes australis*. They proposed that such large zooplankters are dependent on periods of “new” production stemming from the influx of subantarctic waters and wind-mixing.

The three years of *Nyctiphanes australis* data support the view that the subtropical and subantarctic waters and the stability of the water column (Fig. 4) influence the level of *N. australis* production. It seems likely that the dominance of nutrient-poor subtropical water on the entire shelf and the strong stratification in the Maria Island area in the summer of 1989 were responsible for the disappearance of *N. australis*. It was only during late autumn when cooler waters began to intrude from the south and the thermocline began breaking down (which indicated mixing of the water column) that *N. australis* began to reappear. In 1990, EAC water dominated the outer shelf and stratification was weaker, resulting in an increase in the biomass of *N. australis* either from increased production or from immigration. The dominance of subantarctic water and the well-mixed water column in the summer of 1991 resulted in even higher levels of production. Interestingly, a sudden decrease in *N. australis* density and biomass in the autumn of 1991 coincided with an inflow of warmer subtropical water at that time (cf. Figs. 3 and 7), underlining the intimate association between *N. australis* and local hydrography. A further example of this relationship can be found in the fine-scale data, where a decrease in *N. australis* biomass coincided with an influx of EAC water in April 1990.

Relationship to the fishery

ENSO fluctuations are known to affect the distribution and availability of many pelagic species (Sharp and Csirke 1984), including other *Trachurus* species (Pearcy et al. 1985, Smith 1985, Fiedler and Bernard 1987). Smith reported that *T. symmetricus* in the Californian current change their distribution during an El Niño event, but was unsure whether the change was directly related to temperature, or to changes in prey distributions related

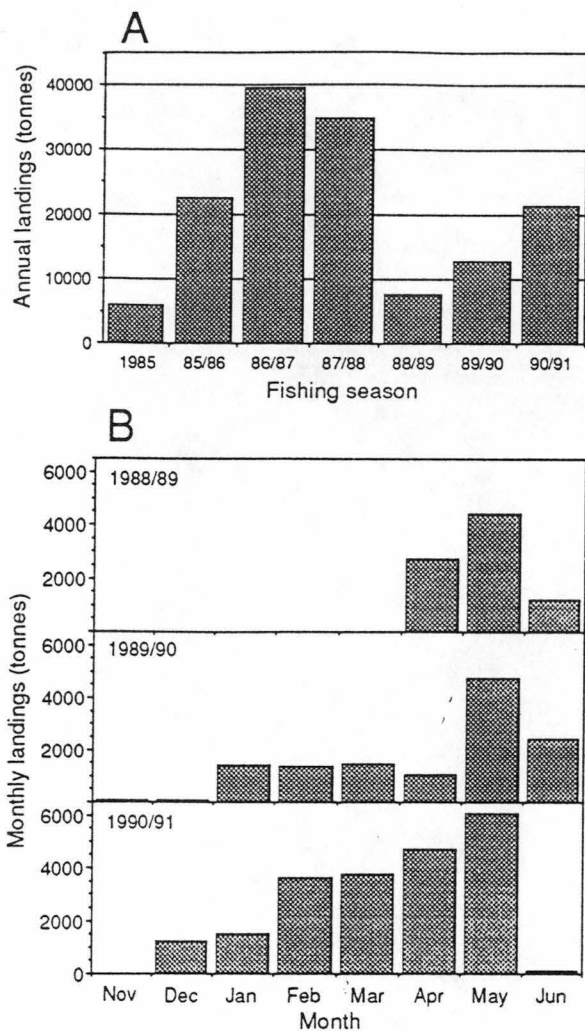


Fig. 9. *Trachurus declivis*. Annual fishery landings between 1985 and 1991 (A) and monthly fishery landings (B) during study period

to temperature. Off Tasmania, Blackburn (1957) found that the success of the barracouta fishery in Bass Strait was closely linked with fluctuations in stocks of *Nyctiphanes australis*. In a study of the seasonal change in schooling behaviour and vulnerability to fishing of *T. declivis* in Tasmanian waters, Williams and Pullen (1993) found that the fishery was based on feeding schools. In their study, both school size and catch rates were highest in autumn, at the time when we found not only the highest densities of *N. australis*, but also the highest stomach fullness values in the stomachs of *T. declivis*.

Our results indicate a close relationship between the biomass of *Nyctiphanes australis* and the availability of *Trachurus declivis* to the fishery off eastern Tasmania. It seems likely, therefore, that changes in the density of the former would affect the schooling behaviour of *T. declivis*, and consequently the amount of fish available to the fishery. We also suggest that *T. declivis* are responding not only to an increase in the biomass of *N. australis*, but also to an increase in the proportion of adult *N. australis* at this time. That *T. declivis* selects positively the

larger size classes of *N. australis* (Fig. 8) supports this contention. Landings of fish overlapped the period of this study (Fig. 9 A) and paralleled the density patterns of *N. australis* over the same period. No landings were made during the summer months of 1989, when *N. australis* density was negligible (Fig. 9 B). The commercial catches in 1990 and 1991 also reflected the relative density of *N. australis* in those years, with more fish being landed in 1991 than 1990 (Fig. 9 A).

In summary, we have shown that the presence and density of *Nyctiphanes australis* in coastal waters of eastern Tasmania are associated with changes in the regional oceanography on both seasonal and interannual scales. Due to the dependence of *Trachurus declivis* on this species, the changing influence of the dominant water masses on the plankton also determines the availability of fish to the *T. declivis* fishery. This is particularly significant during La Niña years, when prey populations are largely absent. An understanding of how these interannual variations in regional oceanography affect the distribution of plankton can lead to valuable input into forecasting returns to the fishery.

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CHAPTER 3

Biomass of zooplankton and micronekton in the southern bluefin tuna (*Thunnus maccoyii*) fishing grounds off eastern Tasmania, Australia

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Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia

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ABSTRACT: The southern bluefin tuna (SBT) supports a seasonal fishery off the east coast of Tasmania, Australia. The distribution of zooplankton biomass in this region was examined as a means of finding out why the SBT are attracted to this area. We examined whether there was a particular area or depth stratum that supported significantly greater amounts of potential feed, directly or indirectly, for SBT. Samples of zooplankton and micronekton were collected during the winter SBT fishery seasons in 1992–94. Five net types (mouth opening 0.25 to ~80 m²) with codend mesh sizes ranging from 100 to 1000 µm were used. Samples were collected from 4 main hydrographic areas: warm East Australian Current water, cool subantarctic water, the front separating them (the subtropical convergence), and the adjacent shelf. Four depth strata (50, 150, 250 and 350 m) were also sampled. In contrast to our expectations, the biomass in the subtropical convergence was no greater than that in the 3 other areas. Rather, it was the shelf, albeit with some inconsistencies, that generally had the greatest biomass of both zooplankton and micronekton. Offshore, there was no significant difference in the biomass of the depth strata sampled, although the biomass of gelatinous zooplankton in the surface waters increased during the study period. We suggest that the higher biomass on the shelf is the result of increased nutrients derived from a mixture of subantarctic water and upwelling along the shelf break. This biomass is converted via krill and gelatinous zooplankton to small pelagics such as jack mackerel, and finally to top predators, amongst which is SBT. The SBT, particularly sub-adults, may time their migration eastward to take advantage of the concentrations of prey present at this time of year.

KEY WORDS: Zooplankton · Micronekton · Biomass · Southern bluefin tuna

INTRODUCTION

It has long been known that tuna aggregate around oceanic features such as eddies and fronts, which are areas of high productivity (e.g. Dufor & Stretta 1973, Shingu 1981, Laurs et al. 1984, Yamamoto & Nishizawa 1986, Fiedler & Bernard 1987, Roger 1994). Fronts are generally thought to have a greater phytoplankton abundance than adjacent waters (Loder & Platt 1985, Peinert & Miquel 1994). They may, therefore, support a higher zooplankton biomass through an increase in the phytoplankton stock (Thibault et al. 1994). For example, frontal waters may provide the best long-term average feeding conditions for herring *Clupea*

harengus larvae (Kjørboe & Johansen 1986). Presumably, therefore, fronts provide better feeding conditions for top predators. Both albacore *Thunnus alalunga* and skipjack *Katsuwonus pelamis* tuna feed extensively in frontal regions (Fiedler & Bernard 1987).

Southern bluefin tuna *Thunnus maccoyii* (SBT) are fished off the east coast of Tasmania, Australia, on a seasonal basis. The fishing masters of tuna longline vessels loosely target the boundary between the subtropical waters of the East Australian Current (EAC) and the cooler subantarctic waters (SAW) to the south (the subtropical convergence, STC) for this species (Shingu 1981). However, we do not know why the SBT are attracted to the east coast of Tasmania. Does the STC provide a feeding ground of enhanced prey abundance or is it something else?

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Although the STC is targeted by longline fishers off the east coast of Tasmania, they are required to operate outside an 18.5 km (10 n mile) coastal exclusion zone. Inside this zone there is a small recreational southern bluefin troll fishery and a jack mackerel *Trachurus declivis* fishery (Williams et al. 1987). Both fisheries are restricted to the continental shelf waters of eastern and southern Tasmania. Jack mackerel—one of the main prey of SBT (J. W. Young, T. D. Lamb, D. Le, R. W. Bradford & W. Whitelaw unpubl.)—is widely distributed over the shelf and shelf break/upper-slope region in autumn (Jordan et al. 1995), which is the start of the SBT longline fishing season. In addition, the shelf region supports a large biomass of the euphausiid *Nyctiphanes australis*, the main prey of jack mackerel (Young et al. 1993). Therefore, the shelf region may also influence the distribution of potential prey for SBT off Tasmania at this time.

The east coast of Tasmania has a complex hydrography. Warm filaments and eddies of the EAC meet cold SAW, creating a broad offshore front—the STC (after Wyrski 1960)—with a surface temperature gradient of ~2 to 4°C (Fig. 1). The latitudinal position of this front varies both seasonally and annually (Harris et al. 1987, Young et al. 1993). On the shelf, apart from periodic intrusions of EAC water, a generally northward flow of SAW mixed with west coast water and river runoff produces a tongue of cold, nutrient-rich water, which can extend the length of the island (Cresswell et al. 1994).

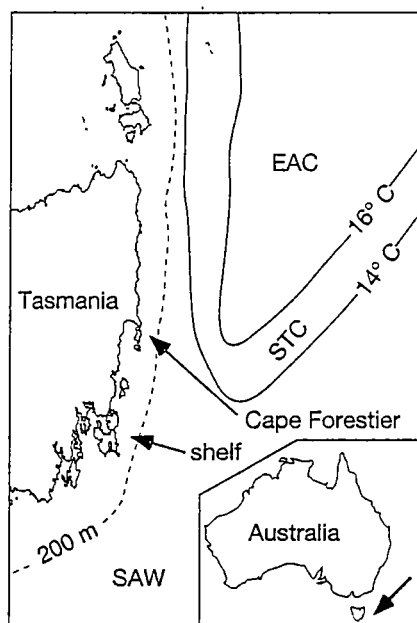


Fig. 1. Diagram of the main sampling areas. STC: subtropical convergence (sensu Wyrski 1960); EAC: East Australian Current; SAW: subantarctic water

Jack mackerel and other prey of SBT are highly mobile, so a quantitative description of their distribution is difficult. In this study, we have therefore examined the distribution of the biomass of prey of the prey of SBT, a technique successfully used by Roger (1994) on tropical tuna. Between 1992 and 1994, nets ranging from small plankton nets to midwater trawls were used to collect zooplankton samples off eastern Tasmania. Sea surface temperature satellite images at the start of the cruise periods and onboard water sampling enabled us to pinpoint the locations of the EAC, STC and SAW, and thus direct our sampling accordingly. We aimed, firstly, to find out whether there were differences in the biomass of zooplankton in the 4 hydrographic areas (EAC, STC, SAW and shelf) off eastern Tasmania. We then aimed to describe the pathway for the transfer of this biomass to top predators, in particular SBT.

METHODS

One cruise was completed each year in May/June of 1992, 1993 and 1994 on CSIRO FRV 'Southern Surveyor' (66.1 m) off the east coast of Tasmania. These cruises were timed to coincide with the autumn/winter longline fishery for SBT. The physical oceanography of the area was described from a series of transects that encompassed EAC water (temperature $T > 16^{\circ}\text{C}$), SAW ($T < 14^{\circ}\text{C}$), the STC ($14^{\circ}\text{C} \leq T \leq 16^{\circ}\text{C}$) and the shelf (≤ 200 m depth) (Fig. 1). On each transect conductivity-temperature-depth (CTD: Neil Brown MK IIIB WOCE) casts to 400 m recorded temperature, salinity, density and nutrients (NO_3 and PO_4). In 1992 and 1993 a SeaBird fluorometer was used to give an indication of chlorophyll *a* to a depth of 150 m. In 1994 fluorescence was recorded directly from the CTD. The oceanographic transects were also used to ground-truth satellite images (Advanced Very High Resolution Radiometer, aboard NOAA's TIROS-N series of satellites) of sea surface temperature taken of the area during each cruise.

Net collections. Five net types were used to sample the zooplankton off the east coast of Tasmania (Table 1). Microzooplankton (animals from 20 μm to 2 mm; classification of Omori & Ikeda 1984) was sampled with a drop net (Heron 1982) of mesh size 100 μm and mouth area 0.25 m^2 at each of the hydrographic stations (Fig. 2). This net sampled to 100 m except on the shelf, where it sampled to 60 m.

Macrozooplankton (animals from 2 to 20 mm) was sampled at night (19:00 to 04:00 h) with a multiple opening/closing BIONESS net (mouth opening 1 m^2) in 1992 and 1993. The frame was fitted with multiple nets of 335 μm mesh. Depth and net-trip time were

Table 1. Net type, mesh size and number of samples collected off the east coast of Tasmania. SAW: subantarctic water, STC subtropical convergence, EAC, East Australian Current. See Fig. 2 for station positions

Net type	Year	Mesh (µm)	No of samples per region				Maximum depth (m)
			SAW	STC	EAC	Shelf	
Drop net	1992	100	26	36	19	22	100
	1993	100	19	7	24	6	100
	1994	100	3	21	2	24	100
BIONESS	1992	335	7	7	2	4	400
	1993	335	5	5	5	3	400
Bongo net	1994	1000	26	17	15	11	200
Surface net	1992	1000	20	11	13	17	<5
	1993	1000	19	16	14	13	<5
	1994	1000	20	30	24	17	<5
IYGPT	1992	Trawl	9	12	3	5	400
	1993	Trawl	10	6	6	2	400
	1994	Trawl	3	2	4	1	400

transmitted to the surface via a conducting tow cable. Each tow consisted of an oblique tow to 400 m followed by oblique tows for 20 min each at depths of 400–300 m, 300–200 m, 200–100 m and 100 m to the surface. Macrozooplankton was sampled by day in 1994 with a paired 70 cm bongo net (a previous study had shown no difference in the biomass of krill from daytime and nighttime samples over the Tasmanian shelf; Young et al. 1993). Volume filtered was recorded with a flowmeter. A submersible data logger attached to the frame transmitted depth, rate of descent and elapsed fishing time. The bongo net fished obliquely from the surface to 200 m and back again over about 20 min.

To sample the surface macrozooplankton, a square surface net (mouth area 1 m² and 1000 µm mesh) fitted with a mechanical flowmeter was deployed with each BIONESS, bongo and IYGPT (International Young Gadoid Pelagic Trawl) midwater trawl net from a 3 m davit rigged amidships.

Micronekton (animals between 2 and 20 cm) was sampled at night (19:00 to 04:00 h) with an IYGPT midwater trawl (mouth area 1 m², mesh size 1000 µm) (see Young & Blaber 1986) fitted with an opening/closing codend (Pearcy et al. 1977). The codend had an electronic timer to trip nets at set times. Depth, mouth opening, headline height and board spread of the trawl were monitored acoustically. In 1992 and 1993 the sampling pattern followed that for the BIONESS net, with a 40 min oblique tow to 400 m, followed by 20 min oblique tows at depths of 400–300, 300–200, 200–100 and 100–0 m. During 1994, the midwater trawl was set to fish two 40 min oblique tows: surface to 400 m and 400 m to surface.

All samples were fixed in 10% formalin in seawater buffered with sodium acetate.

Laboratory analysis. Microzooplankton samples were dried for 24 h at 60°C and weighed (± 0.05 g). Macrozooplankton samples were sorted into fish, cephalopods, crustaceans, and gelatinous zooplankton. A wet weight for each group was recorded. The crustacean fraction was split once with a Folsom splitter and one half was returned to the jar, the other half was dried at 60°C for 24 h or until constant weight was achieved. Micronekton samples were sorted to species level where possible, counted and (wet) weighed. Crustaceans and gelatinous zooplankton were weighed separately.

Where samples were required for identification, dry weight was estimated from wet weight using a conversion factor (Table 2). Replicate samples of represen-

tative taxa were (wet) weighed and then dried at 60°C for 24 h and an average value was used as the conversion factor of wet weight to dry weight. Dry weights were used in all analyses. Our values for dry weights of the main prey taxa corresponded to values established by other researchers (see for example Wissing et al. 1973, Wiebe et al. 1975, Omori & Ikeda 1984, Heron et al. 1988).

Data analysis. Volume filtered by the drop net was calculated by multiplying the depth sampled by the area of the mouth opening. Volume filtered (V) by the surface and bongo nets (in m³) was calculated from the equation $V = DA$ where D is distance travelled (calculated from the flowmeter readings) and A is net mouth area (m²). Volume filtered by the BIONESS and midwater trawl nets was calculated by the equation $V = S \cdot d \cdot A$, where S is ship's speed (m s⁻¹) and d is duration of tow (s). Microzooplankton were expressed as g dry wt per 100 m³, macrozooplankton were expressed as g dry wt per 1000 m³, and micronekton as g dry wt per 100 000 m³. Fluorescence was expressed as standardised fluorescence units (FU) and was taken as an index of phytoplankton biomass.

Comparisons of biomass between years, area and depth were made with a multiway ANOVA (SYSTAT). All data were transformed to $\log_e(\text{dry weight} + 1)$, as

Table 2. Conversion factors used to convert wet weight to dry weight for the 4 main taxa

Group	Conversion
Pisces	0.244
Cephalopoda	0.128
Crustacea	0.171
Gelatinous zooplankton	0.034

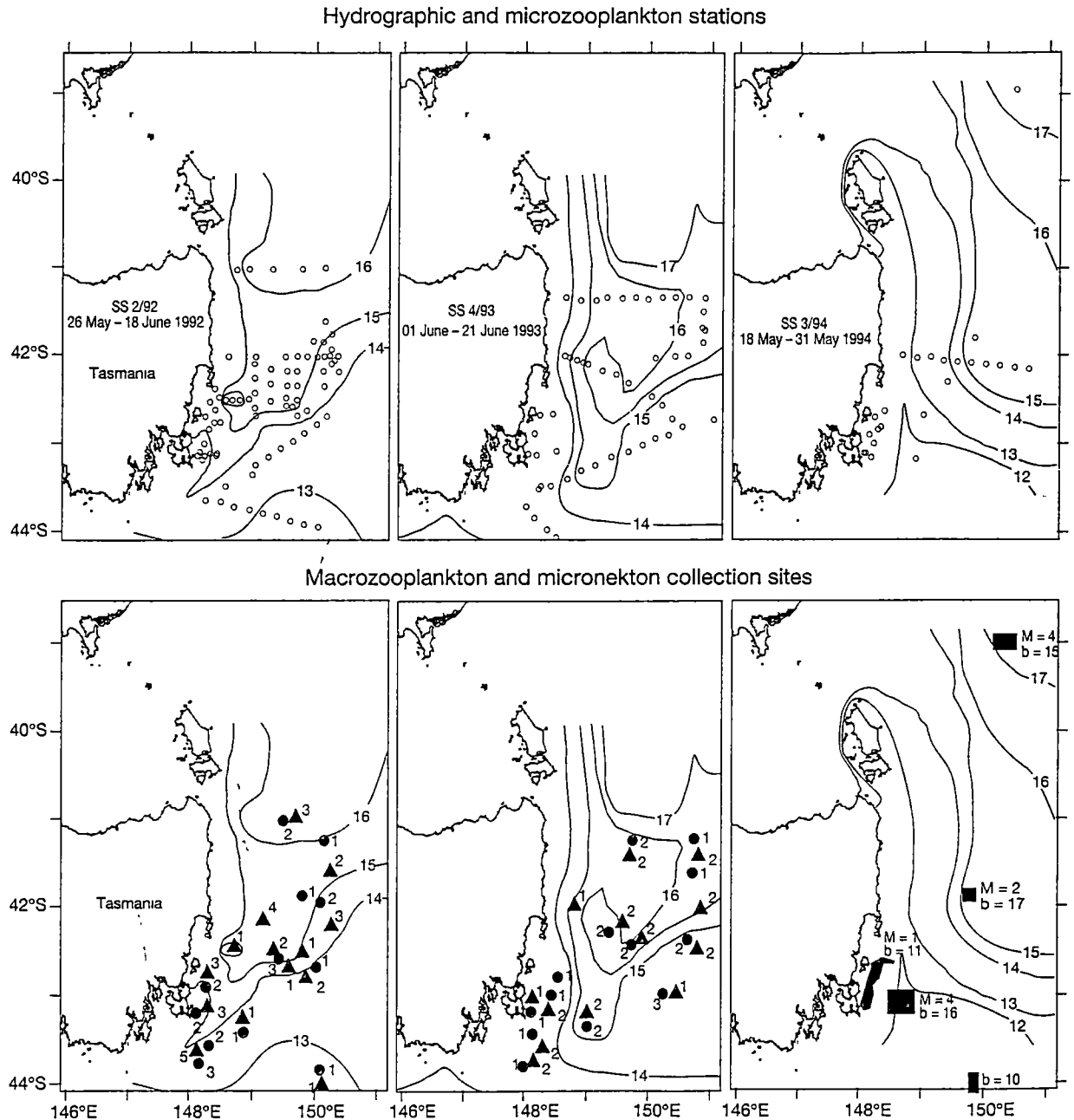


Fig. 2. Station positions for the 3 cruises off eastern Tasmania, Australia. (○) CTD/drop net stations, (▲) IYGPT midwater trawl stations; (●) BIONESS stations. M: IYGPT midwater trawl; b: bongo net (number of stations shown). Surface net samples were collected at each IYGPT midwater trawl, BIONESS and bongo net station. Isotherms refer to temperature in °C

this transformation gave the most even distribution of residuals versus fitted values. A Tukey post hoc test was used to distinguish between groups (Zar 1984). Generally, this test was used when the effects were significant at $p \leq 0.05$, but was also used when a trend was detected ($p < 0.1$ level). Depth comparisons apply to offshore samples only.

RESULTS

Physical oceanography

In June 1992, satellite imagery and our hydrographic data showed a wedge of warm East Australian Current (EAC) water extending down the eastern Tasmanian

shelf to about 43°S. Offshore a broad front (between 14 and 15°C) was present on a NE-SW axis (Fig. 2). To the south, colder subantarctic water (SAW) was present. The following year the EAC was slightly warmer but was further offshore, possibly the result of a cool tongue of SAW pushing northward along the shelf (Fig. 2). Satellite-tracked drifter buoys released in 1992 and 1993 off the west coast of Tasmania identified a current of west coast water on the continental shelf moving eastward (Cresswell et al. 1994). The front was much broader and less intense in 1993 than in 1992. In 1994 the shelf was dominated by a mixture of colder SAW and west coast water (Fig. 2). The front was most pronounced in 1994 with a ~4°C change in surface water temperature over approximately 90 km.

Vertical cross-sections constructed from CTD casts eastward of Cape Forestier (Fig. 1) over the 3 years revealed the presence of 2 main fronts, one at the shelf break and one between EAC and subantarctic waters 120 to 160 km east of the coast (Fig. 3). The intensity of the shelf-break front was less pronounced in 1994 when SAW was more prevalent generally. The EAC was restricted largely to the upper 200 m of the water column, although sloping of isotherms indicated its influence extended to at least 400 m. The nitrate, phosphate and fluorescence transects indicated upwelling of nutrients along the shelf break and subtropical convergence (STC) in 1992 and 1993 (Fig. 3). In 1994 nutrient levels were generally higher, reflecting the dominance of SAW at this time.

Net sampling

A total of 209 drop net, 38 BIONESS, 69 bongo, 214 surface net and 63 IYGPT midwater trawl samples were taken over the 3 years (Table 1). The biomass of microzooplankton ranged from 0 to 172.19 g per 100 m³ ($\bar{x} \pm \text{SE} = 2.26 \pm 1.02$). Macrozooplankton samples ranged in biomass from 0 to 373.84 g per 1000 m³ ($\bar{x} = 6.29 \pm 1.07$). Micronekton samples ranged from 0.67 to 21 301.20 g per 100 000 m³ ($\bar{x} = 476.91 \pm 336.94$).

Composition of biomass

The biomass was composed of 4 broad taxa: gelatinous zooplankton, crustaceans, fish and squid. Of these, gelatinous zooplankton consisted largely of the salps *Thalia democratica* and *Thetys vagina*, and pyrosomes. The crustacean fraction from offshore waters consisted mainly of the decapods *Sergestes* (*Sergia*) *prehen-silis*, *S. (Sergia)* *potens*, *S. (Sergestes)* *arcticus*, *Acantheephyra quadrispinosa* and *Gennadas* spp., and the euphausiids

Euphausia similis var. *armata* and *E. spinifera* (R. Bradford unpubl. data). Shelf catches were dominated by the euphausiid *Nyctiphanes australis*. A total of 109 species of fish identified from offshore consisted largely of myctophid and stomiatoid species (Young et al. in press). Only 38 fish species, of which jack mackerel *Trachurus declivis* was the main one, were identified from the shelf. The squid fraction was dominated by *Lycoteuthis longera*, *Abraliopsis gilchristi* and *Histioteuthis* spp. offshore, and by *Nototodarus gouldi* and *Euprymna tasmanica* over the shelf.

Interannual differences in biomass

Overall, biomass was generally lowest in 1992 and highest in 1994 (Fig. 4a). Microzooplankton biomass changed little from 1992 to 1993. An increase from 1993 to 1994 was not statistically significant (Table 3, Fig. 4a). Similarly, there was little difference in the biomass of macrozooplankton and surface macrozooplankton between 1992 and 1993. Although we were unable to collect BIONESS samples in 1994, the surface net samples showed an increase in that year. Micronekton biomass increased over the 3 years (Fig. 4a).

The main taxa were not separated in the microzooplankton samples. The composition of the BIONESS net samples, which contained mainly crustaceans, did not differ between years (Fig. 4b). In contrast, the surface macrozooplankton samples, mainly crustaceans in 1992, were largely composed of gelatinous zooplankton by 1993 and 1994 (Fig. 4b). Fish taxa dominated the micronekton in 1992. However, the proportion of fish biomass decreased over the following years, while gelatinous zooplankton increased.

Distribution of biomass by area

Microzooplankton (drop net). The biomass of microzooplankton did not differ significantly between years despite it being greater in 1994 (Fig. 4a). However, there

Table 3. Comparisons between years, areas and their interactions of the 5 main biomass groupings off eastern Tasmania using multiway ANOVA (–, no test, bongo nets were used only in 1994, therefore there is no comparison between years)

Net type	Year			Effect			Year × Area		
	df	F-ratio	p	df	F-ratio	p	df	F-ratio	p
Drop net	2	0.62	0.54	3	4.94	0.00	6	3.76	0.00
BIONESS	1	1.38	0.25	3	0.28	0.84	3	1.56	0.22
Bongo net	–	–	–	3	4.76	0.01	–	–	–
Surface net	2	0.16	0.85	3	3.32	0.02	6	2.40	0.03
ITYGPT	2	13.31	0.00	3	4.94	0.00	6	1.44	0.22

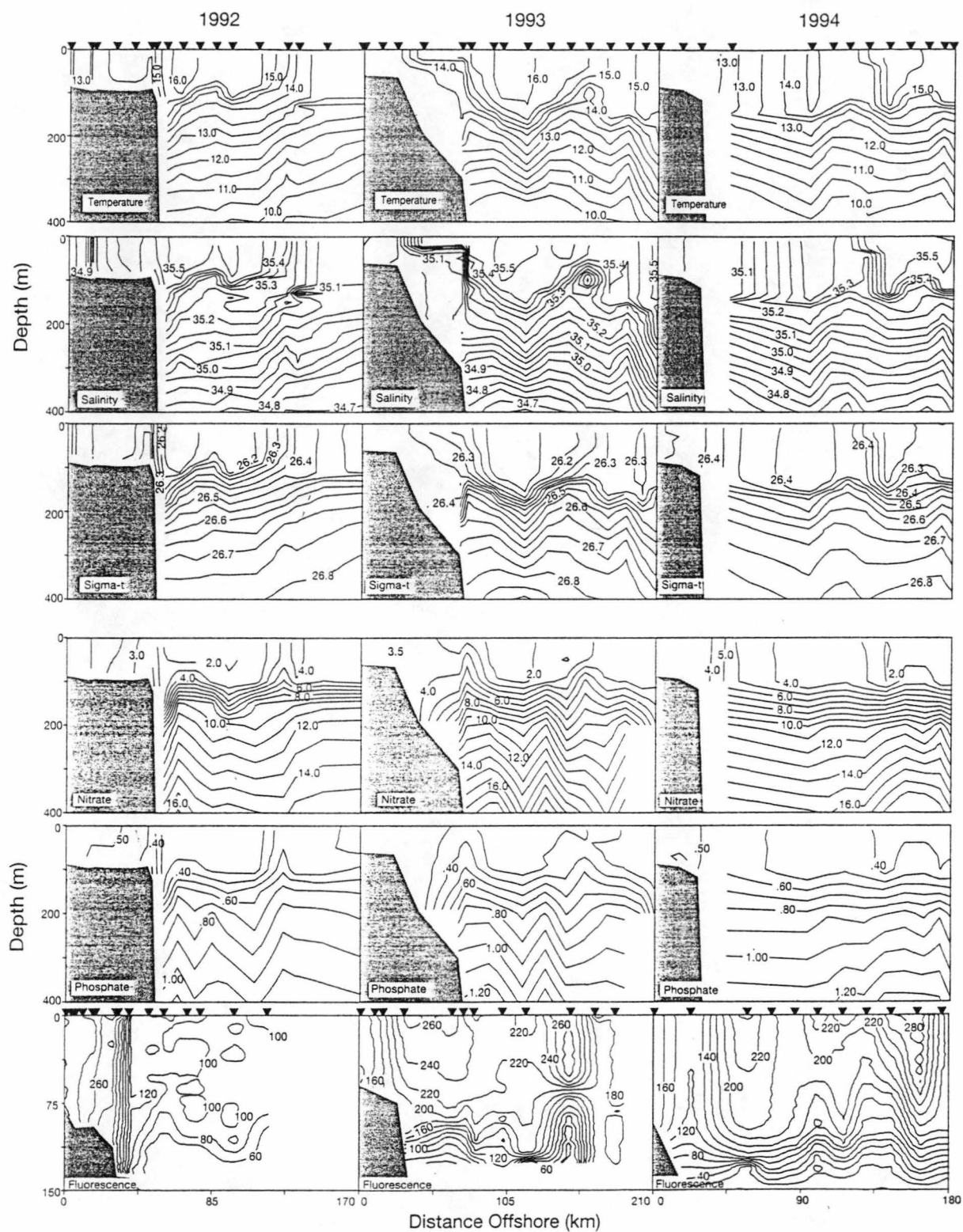


Fig. 3. Vertical cross-sections of the water column to 400 m depth east of Cape Forester showing physical and nutrient parameters constructed from CTD casts. Fluorescence cross-sections are to 150 m. (▼) Position of stations along transect (temperature, °C; salinity, ‰; sigma-t, σ_t ; nitrate, μM ; phosphate, μM ; fluorescence, FU)

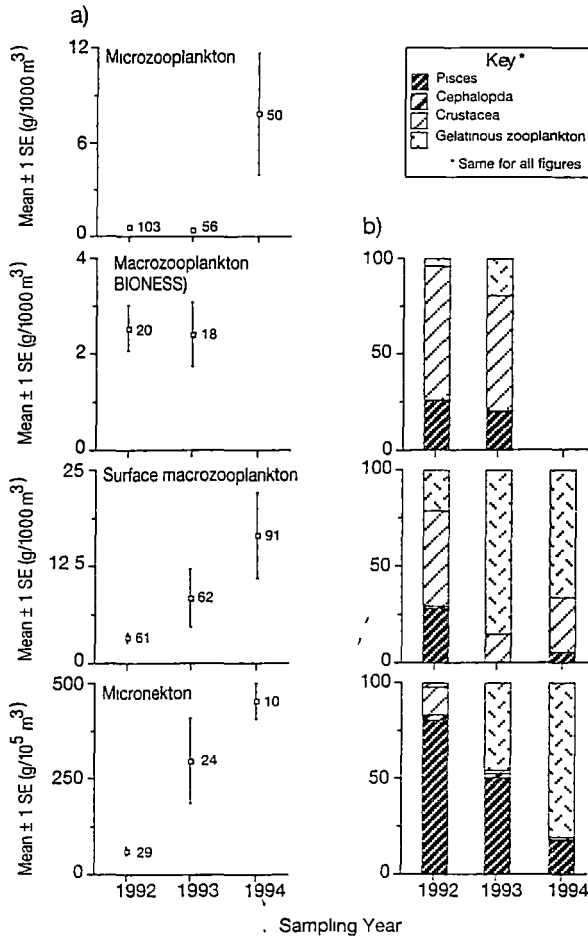


Fig. 4. (a) Comparison of biomass between years for microzooplankton, macrozooplankton and micronekton off eastern Tasmania (mean \pm SE, number = number of stations sampled); (b) percent contribution of the 4 main taxa to the total biomass by year

was a significant difference between areas. Due to a year/area interaction (Table 3, Fig. 5) we analysed the data separately for each year. The biomass over the shelf was significantly different from the other areas (Fig. 5, Table 4). Remarkably, in 1994 the biomass over the shelf was higher by a factor of 10 than in any other area in the 3 years (Fig. 5). This was due to large amounts of gelatinous zooplankton in some samples (one sample contained 770 g wet weight of gelatinous zooplankton).

Macrozooplankton. BIONESS net. No significant difference was found in zooplankton biomass between years or areas (Table 3, Fig. 6a), although over the shelf it was somewhat higher in 1992 than in 1993. The pattern in the percent contribution of the 4 main taxa over the 2 years was consistent (Fig. 6b). Crustacea made up the largest proportion of the macrozooplankton biomass during both years. However, in 1993 the biomass of SAW was dominated by gelatinous zooplankton.

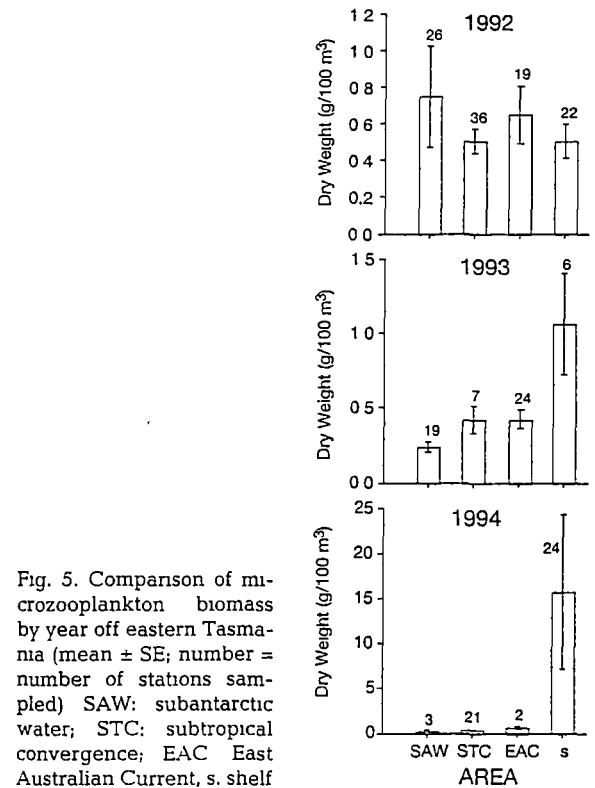


Fig. 5. Comparison of microzooplankton biomass by year off eastern Tasmania (mean \pm SE; number = number of stations sampled) SAW: subantarctic water; STC: subtropical convergence; EAC East Australian Current, s. shelf

Bongo net. The biomass of samples collected from the left and right codends of the bongo net was not significantly different and so was combined for all subsequent analyses (ANOVA, $n = 136$, $df = 1$, $F = 0.49$, $p = 0.49$). Biomass was significantly different between areas (Table 3, Fig. 7a), with biomass over the shelf significantly higher than that collected from the SAW (Tukey, $\bar{x}_b - \bar{x}_a = 0.98$, $q = 3.77$, $df = 65$) and EAC (Tukey, $\bar{x}_b - \bar{x}_a = 1.52$, $q = 5.31$, $df = 6$). Gelatinous zooplankton dominated samples from SAW and shelf waters, whereas Crustacea was the main contributor to biomass collected from the EAC. Gelatinous zooplankton and Crustacea made up similar proportions of the biomass in STC (Fig. 7b).

Surface macrozooplankton (surface net). Macrozooplankton biomass was not significantly different between years but was significantly different between areas (Table 3, Fig. 8a). However, because of the inter-

Table 4. Within-year comparisons of microzooplankton biomass (drop net) between areas (shelf, East Australian Current, subtropical convergence, subantarctic water) off eastern Tasmania using ANOVA

Year	Source	n	df	F-ratio	p
1992	Area	103	3	0.32	0.81
1993	Area	56	3	9.73	0.00
1994	Area	50	3	3.51	0.02

action between area and year, biomass was analysed separately each year. Biomass was highest over the shelf in all 3 years and was significantly higher than SAW and EAC water in 1993 and SAW in 1994 (Table 5). The shelf was dominated by gelatinous zooplankton in 1993 and 1994. The biomass in the SAW was dominated by the crustacean *Euphausia spinifera* in 1994 (Fig. 8a); that species comprised over 60 % of the total biomass in that year.

Micronekton (IYGPT midwater trawl)

The biomass of micronekton differed significantly both between years and between areas with no significant year/area interaction (Table 3). Biomass in 1992 was significantly lower than that collected in 1993 and 1994 (Table 6) (Fig. 4). A Tukey post hoc test indicated that the SAW and shelf had a greater biomass than the EAC (Table 6, Fig. 9a). Gelatinous zooplankton was the dominant taxon collected from SAW and the STC, contributing more than 50 % to the dry weight of the samples (Fig. 9b). In contrast, fish made up more than 50 % of the biomass from the EAC water and the shelf.

Taken separately, the biomass of micronekton in 1992 was relatively consistent across areas (Table 7, Fig. 10a). In contrast, biomass was significantly different between areas in both 1993 and 1994 (Table 7). The biomass over the shelf in 1993 was greater than that of the EAC sampled in that year (Tukey, $\bar{x}_b - \bar{x}_a = 3.18$, $q =$

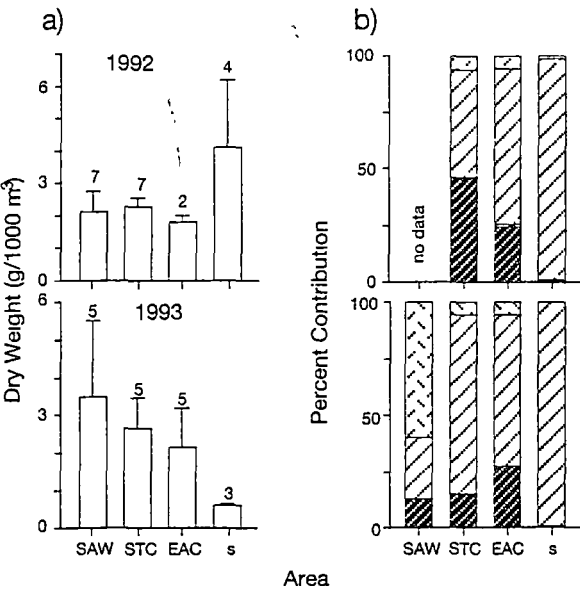


Fig. 6. (a) Comparison of macrozooplankton (BIONESS) biomass by area off eastern Tasmania (mean \pm SE; number = number of stations sampled); (b) percent contribution of the 4 main taxa to the total biomass by area (refer to key in Fig. 4)

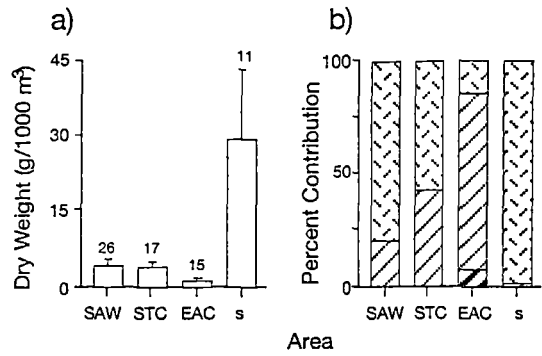


Fig. 7. (a) Comparison of macrozooplankton (bongo net) biomass by area off eastern Tasmania (mean \pm SE; number = number of stations) (b) percent contribution of the 4 main taxa to the total biomass by area (refer to key in Fig. 4)

5.61, $df = 20$). There was a trend for higher biomass over the shelf than the SAW ($p = 0.07$). The shelf had a far greater percentage of fish taxa than the other areas sampled in 1993 (Fig. 10b). The main fish taxon over the shelf was jack mackerel *Trachurus declivis*.

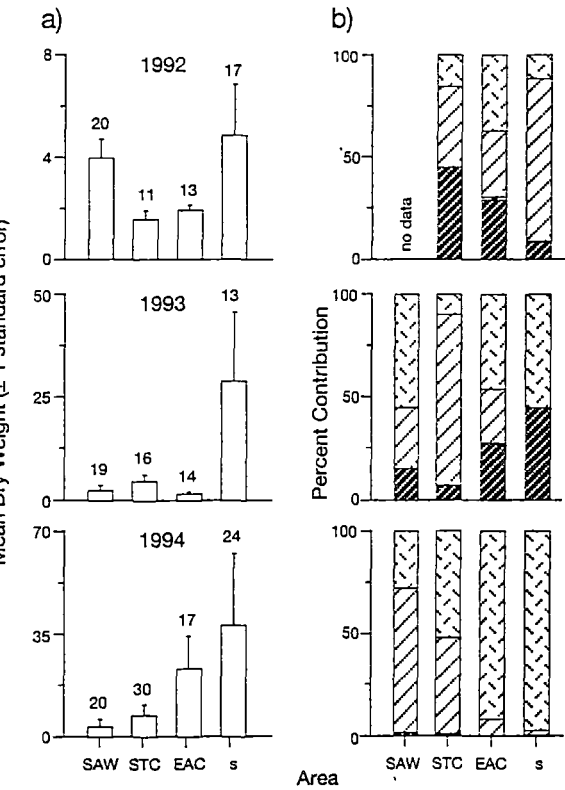


Fig. 8. (a) Comparison of surface macrozooplankton biomass by area off eastern Tasmania (mean \pm SE; number = number of stations sampled); (b) percent contribution of the 4 main taxa to the total biomass by area (refer to key in Fig. 4)

Table 5. Within-year comparisons of macrozooplankton biomass (surface net) between areas (shelf, East Australian Current, subtropical convergence, subantarctic water) off eastern Tasmania using ANOVA

Year	Source	n	df	F-ratio	p
1992	Area	61	3	2.59	0.06
1993	Area	62	3	3.46	0.02
1994	Area	91	3	2.78	0.05

Table 6. Pairwise comparisons of micronekton biomass (IYGPT midwater trawl) by year and using the Tukey test. SAW: subantarctic water; EAC: East Australian Current

Test	$ \bar{x}_b - \bar{x}_a $	SE	q	Error df	p
1993 > 1992	1.81	0.23	7.84	51	0.00
1994 > 1992	1.74	0.31	5.67	51	0.00
Overall SAW > EAC	1.34	0.29	4.58	51	0.02
Shelf > EAC	2.12	0.38	5.64	51	0.01

Table 7. Within-year comparisons of micronekton biomass (IYGPT midwater trawl) between areas (shelf, East Australian Current, subtropical convergence, subantarctic water) off eastern Tasmania using ANOVA

Year	Source	n	df	F-ratio	p
1992	Area	29	3	0.62	0.61
1993	Area	24	3	5.72	0.00
1994	Area	10	3	9.32	0.01

Table 8. Comparisons of macrozooplankton biomass (BIO-NESS net) between depth strata (0–100, 100–200, 200–300, 300–400 m) off eastern Tasmania using ANOVA

Year	Source	n	df	F-ratio	p
Overall	Strata	58	3	0.69	0.56
1992	Strata	27	3	1.14	0.53
1993	Strata	31	3	0.63	0.60

A different pattern in biomass was evident in 1994. The biomass of the SAW was significantly greater than that of the EAC (Tukey, $\bar{x}_b - \bar{x}_a = 2.50$, $q = 6.85$, $df = 6$; Fig. 10a). The biomass of the SAW tended to be greater than that over the shelf ($p = 0.06$). Gelatinous zooplankton, with a few fish taxa, contributed most to the biomass within the SAW (Fig. 10b). The biomass of micronekton within the EAC, on the other hand, was composed mainly of the non-myctophid fish taxa *Bathylagidae* and *Tetragonurus* spp.

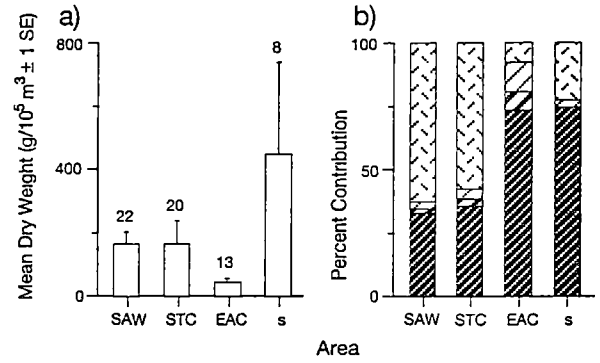


Fig. 9. (a) Comparison of micronekton (IYGPT) biomass by area off eastern Tasmania (mean ± SE). (b) Percent contribution of the 4 main taxa to the overall biomass by area (refer to key in Fig. 4)

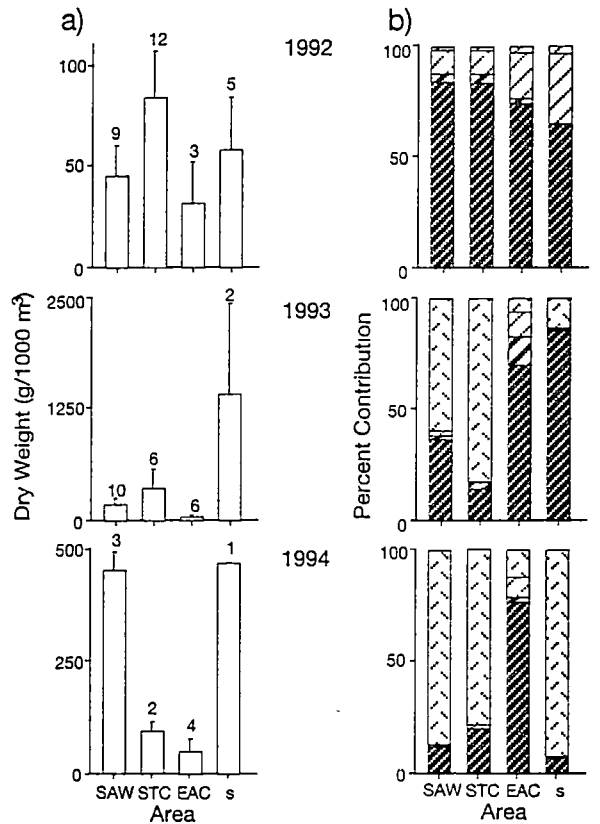


Fig. 10. (a) Comparison of micronekton (IYGPT) biomass by area off eastern Tasmania (mean ± SE; number = number of stations sampled); (b) percent contribution of the 4 main taxa to the total biomass by area (refer to key in Fig. 4)

Vertical distribution of biomass

Macrozooplankton biomass did not differ between strata either overall or within each year (Table 8).

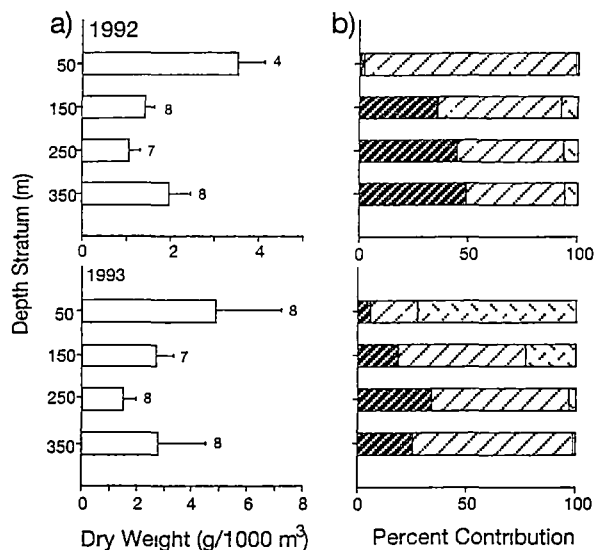


Fig. 11. (a) Vertical distribution of macrozooplankton (BIO-NESS) biomass off eastern Tasmania (number = number of samples per depth stratum); (b) percent contribution of the 4 main taxa to the total biomass per stratum (refer to key in Fig. 4)

Fig. 11a suggests the biomass decreased slightly in the mid-strata in both years, but this was not significant. In 1992 the surface stratum was dominated by crustaceans (Fig. 11b). In contrast, gelatinous zooplankton dominated surface waters in 1993. The lower strata contained an even mix of fish and Crustacea in both years (Fig. 11b).

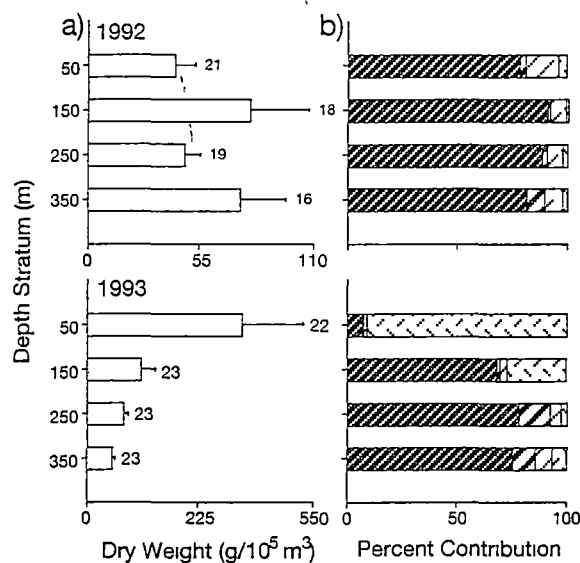


Fig. 12. (a) Vertical distribution of micronekton (IYGPT) biomass off eastern Tasmania (number = number of samples per depth stratum); (b) percent contribution of the 4 main taxa to the total biomass per stratum (refer to key in Fig. 4)

The distribution of micronekton biomass with depth was similar in 1992 and 1993 (there was no depth-stratified sampling in 1994) (Fig. 12a). No significant differences in biomass with depth stratum were found within each year (ANOVA: $n = 74$, $df = 3$, $F = 0.09$, $p = 0.97$; $n = 91$, $df = 3$, $F = 0.59$, $p = 0.62$; 1992 and 1993 respectively).

Trachurus declivis, Bathylagidae, *Lampichthys procerus*, *Lampanyctus australis* and *Diaphus danae* were the most numerous fish taxa in the surface stratum during 1992, with progressively more Stomiformes deeper in the water column. In 1993 the surface stratum was dominated by gelatinous zooplankton, which contributed substantially more to the biomass of the upper 200 m of the water column during 1993 than in 1992 (Fig. 12b). Fish, particularly *Diaphus danae*, *Lampichthys procerus* and *Lampanyctus australis*, dominated the lower stratum in that year.

DISCUSSION

Importance of the shelf

The relatively higher zooplankton biomasses we found inshore were similar to those found for other comparisons of inshore and offshore waters. This is not surprising, as production in coastal waters is generally higher than in open ocean waters, particularly in tropical and oligotrophic systems (e.g. Gncc & Hart 1962, Ortner et al. 1977, Tranter & Kerr 1977, Wiebe et al. 1985), but also in temperate waters (Pillar 1986, Fiedler & Bernard 1987). For example, in shelf waters of the central Californian (USA) coast, upwelling results in an environment rich in phytoplankton that supports fisheries for albacore *Thunnus alalunga* and skipjack tuna *Katsuwonus pelamis* (Fiedler & Bernard 1987). Stomachs of albacore from this area contained a high percentage of krill *Nyctiphanes simplex* and anchovy *Engraulis mordax* (Bernard et al. 1985). Similarly, off South-Western Cape, South Africa, higher zooplankton biomasses have been reported for inshore compared with offshore waters (Pillar 1986). Important pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* fisheries are also found in the same area (Shannon & Field 1985).

The greater biomass in shelf waters off eastern Tasmania appears to be driven largely by the complex of currents that feed the shelf area. Satellite-tracked buoys revealed west coast water, augmented by river run-off, flowed eastward around Tasman Island onto the shelf during autumn (Cresswell et al. 1994). Added to this is the supply of nutrient-rich SAW driven onto the shelf by the prevailing southwesterly winds. Also, upward sloping of isopycnals along the inner edge of

the EAC may draw nutrient-rich slope water onto the shelf (Harris et al. 1987). Our oceanographic transects identified a shelf-break front with relatively higher chlorophyll *a*, which indicated that upwelling was likely in the area. Significantly, autumn blooms of phytoplankton have previously been identified in the same region (Harris et al. 1987). The resulting primary production is food for large stocks of krill *Nyctiphanes australis*, which are most abundant at this time (Young et al. 1993). When the shelf waters of eastern Tasmania were displaced by the intrusion of EAC water in the austral summer-autumn of 1988/89, krill stocks (normally abundant at that time) were absent. The result was the collapse of the jack mackerel fishery that year (Young et al. 1993). A similar pattern of shelf-break upwelling off SW Africa, identified by upward-sloping isotherms, provides nutrients for large stocks of krill, including the congeneric species *Nyctiphanes capensis* (Barange & Pillar 1992).

Subtropical convergence

One of the significant features of this study was the similarity in the biomass of the STC and the surrounding ocean waters (the only real difference was in 1994 when the micronekton biomass of the SAW was significantly higher than that of the surrounding water masses; Fig. 9a). This finding is in contrast to the many studies of oceanic fronts and eddies that have found such areas are sites of greater biomass and productivity (Uda 1973, Bradford et al. 1982, Roman et al. 1985, Heilmann et al. 1994). However, during autumn/winter (when this study was run) such increases in biomass were not always observed (see for example Pingree et al. 1976, 1978), apparently because the depth of the mixed layer increased, imposing a light limitation on the primary productivity. Nevertheless, in a recent study of the STC off South Africa during the austral winter, the biomass within the STC was higher than that of the surrounding waters (Pakhomov et al. 1994).

That the STC was not noticeably different from surrounding areas in the present study appears to be related to the weak gradients of physical (e.g. temperature and salinity) variables between the EAC and SAW. Temperature changes of as little as 1°C per 18 km (10 n mile) were common and sharp discontinuities were rare. Enhanced biological activity, particularly primary productivity, along oceanic fronts is often related to the secondary circulation associated with the frontal region (Videau et al. 1994). For example, eddy-forced upwelling is thought to be the single largest vector for the input of nitrate into surface waters of the Cape Hatteras, North Carolina (USA) region (Yoder et al. 1981). The lack of any strong gradients offshore

may have limited the amount of such secondary circulation in waters off Tasmania. Also, the greater depth of the mixed layer, frequently reaching 300 m in winter (Harris et al. 1987), could result in lower productivity.

In contrast, the strong gradients along the shelf break observed during the 1992 and 1993 autumn cruises suggest upwelling in the shelf-break region. Harris et al. (1987) found an increase in nitrate and phytoplankton along the shelf during autumn, which they believed was linked to the movement of slope water onto the shelf. Occasional increases in phytoplankton biomass, associated with sharp gradients in physical variables, have been reported along the shelf-break off Nova Scotia, Canada (Fournier et al. 1979). In 1994 SAW dominated the waters off the east coast of Tasmania both inshore and offshore, limiting the development of a shelf-break front.

Vertical distribution

In oceanic waters, the biomass of zooplankton generally decreases with depth (Angel & Baker 1982, Wishner 1980). However, we found no evidence of such a decline over the depth ranges we sampled, but we did find that the composition of the biomass changed over the study period. The gelatinous zooplankton in the surface strata were more abundant in 1993 than 1992, while the relative composition of the main taxa changed little in the lower strata. Gelatinous zooplankton accounted in 1993 for about 90% of the micronekton biomass in the upper 100 m. Although we did not sample with respect to depth strata in 1994, the continued presence of significant quantities of gelatinous zooplankton in oblique and surface hauls indicates that SAW was increasing in influence over the study period.

Interannual differences

Overlying the broad differences in biomass between inshore and offshore was a progressive increase in biomass over the 3 years (Fig. 4). This increase appeared to be the result of changes in the regional oceanography and may be related to the general wind strength. A roughly 10 yr cycle in westerly wind strength has been documented for this region (Pook 1992, Thresher 1994). Forecasting the strength of surface westerlies in the Tasmanian region has been linked to differences in geopotential height at 500 hPa (Trenberth 1979, Pook 1992). The mean zonal index (Δ geopotential height) calculated for the 5 mo (December to April) before each cruise increased progressively from about 545 dm (decametres) in 1991/92 to 580 dm before the last

cruise (M. J. Pook unpubl. data). That the EAC moved offshore during the same period supports this view.

The increase in biomass over the study period was due largely to the increased numbers of gelatinous zooplankton, particularly in the upper stratum of the water column and on the shelf. Gelatinous zooplankton can respond quickly to increased nutrient loads through rapid reproduction linked with a short generation time (Heron 1972a, b, Deibel 1985, Kashkina 1986).

Relationship between SBT and plankton

The relationship between plankton stocks and tuna concentrations has previously been demonstrated on fine and broad scales (e.g. Fiedler & Bernard 1987, Roger 1994). Roger (1994) found that in the fishing grounds of tropical tunas, zooplankton biomass was 4 times higher than in latitudes to the south and north. He also found that the biomass of zooplankton, which are either prey or lead to prey of these tuna, was 7 times higher in the same area. Although no plankton data were presented, Hearn (1986) proposed that summer upwellings off South Australia provided an 'extensive area of nutrient-rich water [forming] the basis of a food chain that attracts SBT'.

Off eastern Tasmania, the only area where significantly higher biomasses of plankton were found was over the shelf. If we accept that the autumn/winter migration of SBT to areas off eastern Tasmania is in response to significant quantities of suitable prey, then the importance of the shelf becomes apparent. In an earlier study we found the biomass of krill *Nyctiphanes australis* over the shelf increased in autumn (Young et al. 1993), which led to schooling of their main predator, jack mackerel (Williams & Pullen 1993), itself an important prey of SBT (Young et al. unpubl.). We suggest, therefore, that juvenile SBT time their migration eastward from south Australia to take advantage of the autumn production generated on the shelf. Fishery data indicate that by mid-winter the longline vessels have moved northward at a time when the krill stocks decline.

The link between krill, jack mackerel and SBT is well established for the inshore waters of eastern Tasmania. However, *Nyctiphanes australis* is rarely found offshore, while salps are distributed widely in inshore and offshore waters of southeastern Australia (Thompson 1948). Salps, which can respond rapidly to increases in nutrients and phytoplankton, act as a major energy store and also transfer nutrients to higher trophic levels (Deibel 1985, Caron et al. 1989). Salps may therefore provide one of the initial links between primary and secondary production in the early stages of offshore (and inshore) phytoplankton blooms

(Deibel 1985). Furthermore, in areas where nutrient and hydrographic requirements sustain high biomasses of salps for extended periods, salps themselves can play a significant and sometimes leading role in fish nutrition (Kashkina 1986, Heron et al. 1988). The presence of gelatinous zooplankton in the stomachs of SBT and their prey during the study period (Young et al. 1994) adds support to this idea.

In conclusion, nutrient-rich subantarctic and west coast water augmented by shelf-break upwelling appears to be linked to higher biomasses of zooplankton and micronekton over the shelf region. In particular, the shelf region is characterised by high biomasses of *Nyctiphanes australis* and gelatinous zooplankton, both of which figure largely in the diet of jack mackerel, an important prey of SBT. Offshore, the pathway of energy transfer between primary production and top predators is less clear. However, gelatinous zooplankton may be an important link between primary production and SBT.

Addendum. A recent debate has arisen on the naming of the water masses we have described. It has been proposed that the subtropical convergence described herein may be the northern edge of a broader subtropical convergence zone (L. Clementsen, CSIRO, unpubl. data). Hence, what we have called subantarctic water may actually be the subtropical convergence zone.

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CHAPTER 4

Distribution and community structure of midwater fishes associated with the subtropical convergence off eastern Tasmania, Australia

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Abstract Midwater fishes were sampled at night to a depth of 400 m in oceanic waters east of Tasmania, Australia, in May/June of 1992, 1993 and 1994. We examined whether there were differences in the distribution and density of these fishes in relation to the subtropical convergence (STC) separating East Australia Current (EAC) water from subantarctic water (SAW) to the south. A total of 23 999 fishes from 107 taxa and 43 families were identified. Four new records were identified from the study area. Myctophids and stomiatoids were the main fish taxa captured. We found no evidence of increased density of the combined fish catch in any particular area. However, differences between areas in the density of individual species were noted, although no species was confined to any one area. *Ceratoscopelus warmingi*, *Lobianchia dofleini* and *Vinciguerrria* spp. were most abundant in the EAC, whereas *Lampichthys procerus* was most abundant in the SAW. Only *Diaphus danae* was found in significantly higher numbers in the STC. Multivariate analysis revealed that community structure in the EAC was significantly different from that of the SAW but not from the STC. Further, when separated by depth, the shallow EAC group was significantly different in all group comparisons bar that with the shallow STC. Our data indicated that the thin EAC layer above 200 m could be distinguished by its fauna from the SAW. However, we could not detect a separate community in the STC. We conclude, therefore, that the STC is not an area of increased micronekton abundance, nor does it contain a distinct community, during the Australian autumn/winter.

Introduction

Micronektonic fishes are one of the main components of the upper levels of the oceanic water column at night (Karnella 1987). They are also known to selectively occur with concentrations of other pelagic taxa (Auster et al. 1992). Unlike micronektonic fishes, however, some of these other taxa (e.g. squid) are known to largely avoid traditional capture techniques such as midwater trawling (Roger 1994). Therefore, knowledge of the distribution and abundance of these fishes can also provide a more general indication of oceanic productivity. Micronektonic fishes also show significant differences in species composition and community structure in relation to the depth, or the water mass, in which they are found (Brandt 1981, 1983; Brandt and Wadley 1981). They can therefore, be useful in identifying differences between neighbouring or overlapping water masses.

Off eastern Tasmania, warm, nutrient-poor East Australia Current (EAC) water meets cooler nutrient-rich subantarctic water (SAW), creating the subtropical convergence (STC) (Wyrtki 1960) (present Fig. 1), the latitudinal position of which varies both seasonally and between years (Harris et al. 1987). During the Australian summer, the EAC extends southward, retreating again in winter (Newell 1961). Overlying the seasonal signal are interannual fluctuations relating to both the El Niño Southern oscillation and the strength of the prevailing westerly winds (Harris et al. 1987; Young et al. 1993). Such boundary regions can be areas of increased productivity which can result in increased diversity and abundance of both fauna and flora (see review in Olson and Backus 1985). They can also mark the boundary between different species or species groups (Robertson et al. 1978), although this may not always be the case (McKelvie 1985). There are numerous examples of top predators, such as tunas, being caught in these areas (Laurs et al.

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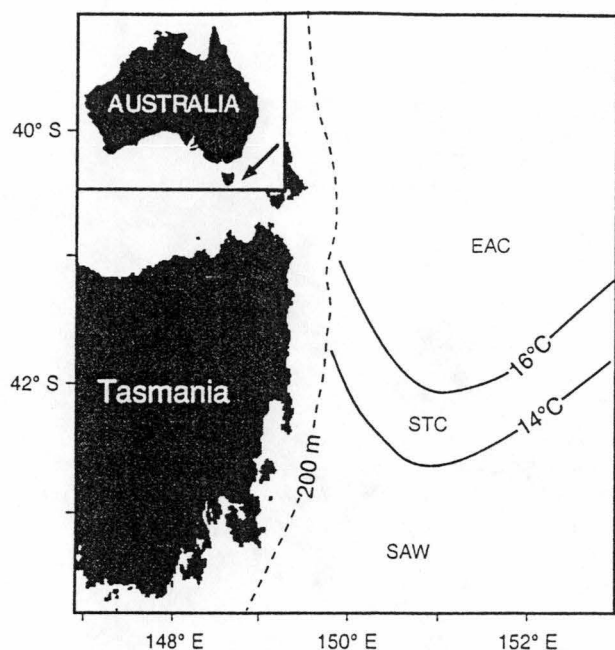


Fig. 1 Major water masses off eastern Tasmania, Australia (SAW subantarctic water; STC subtropical convergence; EAC East Australian Current)

1984; Fiedler and Bernard 1987; Reddy et al. 1995). It is assumed that tunas aggregate in these areas to take advantage of increased prey abundance (Sund et al. 1981; Laurs et al. 1984; Fiedler and Bernard 1987). However, such an hypothesis has rarely been tested.

The east coast of Tasmania is the home of an important southern bluefin tuna (SBT) fishery. Apart from filling a seasonal quota of 1500 t this area is also important in assessment of the overall SBT stock, as tag-returns indicate that eastern Tasmania is an important destination along their migration route (Shingu 1981). One hypothesis given for the aggregations of southern bluefin tuna in this area is that increased nutrients in the region, derived from vertical and lateral mixing of adjacent water masses, provides an environment for aggregations of micronekton, and hence increased prey levels.

The aims of this study, therefore, were to (1) determine the position and vertical (physical) structure of the SAW, STC and EAC, down to 400 m, off eastern Tasmania between 1992 and 1994; (2) compare the density and horizontal distribution of the main fish taxa inhabiting these waters; (3) describe the night-time depth distributions of the main fish taxa from the surface to 400 m; (4) determine whether the community structure of midwater fishes off eastern Tasmania differed between the SAW, STC and EAC.

Materials and methods

Sampling

Between 1992 and 1994, three cruises (26 May to 18 June 1992; 1 to 21 June 1993; 18 to 31 May 1994) were completed on F.R.V. "Southern Surveyor" in waters off eastern Tasmania (Fig. 2) to coincide with the annual Japanese longline fishery. Three years of data were thought necessary because of the interannual variability in the strength and position of the STC (Harris et al. 1987). Each cruise was planned to sample the major water masses and the STC via a series of west to east and north to south transects. Along each transect, at intervals of between 5 and 30 nautical miles, conductivity-temperature-depth (CTD) casts were made to a maximum depth of 1000 m.

Replicate tows from the surface to 400 m were made at night with an IYGPT midwater fish-trawl (see Young and Blaber 1986), fitted with an opening-closing cod end (mesh size 1 mm; Percy et al. 1977). In 1992 and 1993, five depth strata were fished: surface to 400 m (oblique); 400 to 300; 300 to 200; 200 to 100 and 100 to 50 m from the surface. Each oblique tow lasted for 40 min, with the ensuing depth-stratified tow lasting 15 min. In 1994, we fished from the surface to 400 m over 40 min, closed the net, and then fished for the same time to the surface. Typically, trawls were towed at 3 knots and filtered $\approx 170\,000\text{ m}^3$ of water at each depth stratum. Net sampling was restricted to night (19:00 to 04:00 hrs) to minimise net avoidance and to account for the shallow night distributions of most midwater fish (Karnella 1987). Samples were preserved in 10% formalin in seawater buffered with sodium acetate.

Laboratory analyses

Trawl collections were transferred to 70% ethanol and identified, counted and weighed ($\pm 0.5\text{ g}$). Biomass data are compared elsewhere (Young et al. 1996). Fishes were identified using keys in Smith and Heemstra (1986), Baird (1971) and the unpublished myctophid key by Dr. J. Paxton (Australian Museum). The stomiiform genus *Vinciguerria* was comprised of three species; *V. attenuata*, *V. nimbaria* and *V. poweriae*. Of a subset of 156 individuals, 147 (94.2%) were *V. attenuata*, two (1.3%) were *V. nimbaria* and seven (4.5%) were *V. poweriae*. However, as the condition of many of these individuals was poor, we grouped the genus under the one taxon. The individual presented as *Lampanyctus* sp. may be a new species, and as such was registered in the I.S.R. Munro fish collection at CSIRO. Some taxa were not identified beyond genus level, mainly because uncertainties surrounding their taxonomy made identification to a lower level equivocal (e.g. some genera of the family Melanostomiidae).

Data analysis

Volume filtered (m^3) by the net was calculated from the formula:

$$W \times H \times (T \times 60) \times (S \times 0.514444),$$

where W = net width or wingspread (m), H = net headline height (m), T = time in minute, s and S = ship speed in nautical miles per hour. Raw fish data were standardised to numbers per 10^3 m^3 . Stations were divided by position with respect to the major front into SAW ($< 14^\circ\text{C}$), STC (> 14 to $< 16^\circ\text{C}$) and EAC ($> 16^\circ\text{C}$) waters using satellite imagery and ground-truthing from F.R.V. "Southern Surveyor" (Wyrski 1960; Young et al. 1996).

Initially, the ten most abundant taxa and the main groups of "all fishes" total myctophids and total Stomiiformes were compared between areas, depths and years using analysis of variance

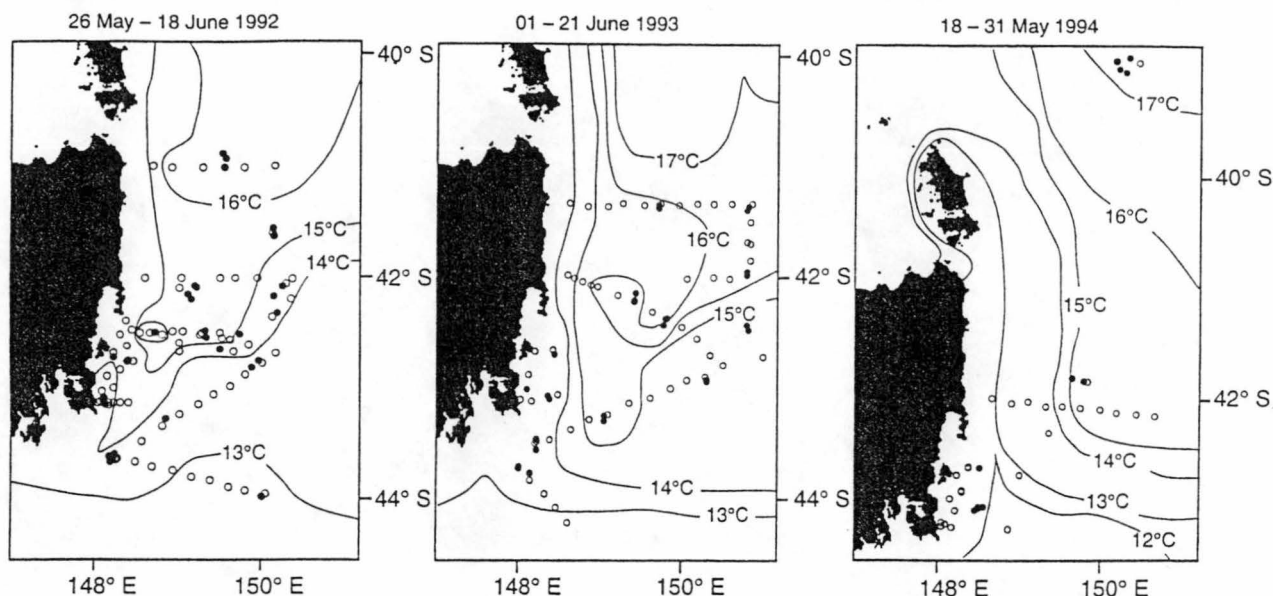


Fig. 2 Study area showing position of CTD casts (○) and trawls (●) off eastern Tasmania, Australia, between 1992 and 1994. Sea-surface temperatures were derived from satellite imagery and ground-truthed by CTD data

(ANOVA). A post-hoc Tukey test was used to determine which groups differed significantly from each other (Zar 1984). The data were transformed to $\log(x + 1)$, as this gave the most even distribution of residuals versus fitted values.

To examine differences in species composition between areas and between depth-strata one-way multivariate analysis of variance (MANOVA) and, linear discriminant-function analysis (DISCRIM) were used. Data were transformed to $\log(x + 1)$. To satisfy the assumptions of sample size required for MANOVA, the number of species used in each analysis was limited to species with $> 1\%$ of the overall density (Tabachnik and Fidell 1989). Roy's greatest characteristic root (gcr) was used as a simultaneous test statistic to compare contrasts between area or depth groups with results for the overall tests (Bird and Hadzi-Pavlovic 1983). Contrasts were considered significant when the contrast statistic θ ($1 - \theta_1$) exceeded the critical value of $R_{0.05}$ ($1 - R_{0.05}$), where $\theta_1 = \text{Roy's } gcr$ for the contrast and $R_{0.05}$ = the critical gcr for the overall test (Bird and Hadzi-Pavlovic 1983). The critical values of Roy's gcr were obtained by interpolation from the tables of Harris (1985).

Community differences were further examined using DISCRIM, which is constrained to maximise the separation between pre-defined groups of samples while minimising the within-group variation (Ter Braak and Prentice 1988). The relative contribution of each species to the structure of the community was assessed using canonical correlations. These were interpreted as important when they exceeded ± 0.3 (Tabachnik and Fidell 1989). Discriminant functions were calculated using the density of each species present. First and second discriminant functions were plotted against each other as these exhibited the most variation.

Results

Physical oceanography

The physical and biological oceanography of the study area between 1992 and 1994 has been described in

detail by Young et al. (1996). Briefly, in June 1992 satellite imagery and our hydrographic data showed a wedge of warm East Australian current water (EAC) extending on to the Tasmanian shelf to $\approx 43^\circ\text{S}$. Offshore, a front with an approximately 2°C change in surface-water temperature over a distance of 20 nautical miles was present on a northeast-southwest axis (Fig. 2). To the south, colder ($\approx 13^\circ\text{C}$) subantarctic water (SAW) was present. During the 1993 sampling period, the subtropical convergence (STC) was slightly warmer, penetrated further south, and extended further offshore. The surface-temperature gradient across the STC was considerably weaker, $\approx 2^\circ\text{C}$ over 100 nautical miles. In 1994, the STC had moved still further offshore and had a surface-temperature gradient of 4°C over 50 nautical miles, the steepest temperature gradient of the three years.

CTD transects made in an easterly direction across the STC (Fig. 3) had shown that the overlying tongue of EAC water was quite shallow, penetrating $< 150\text{ m}$ into the water column. Temperature-salinity plots from the three sampling regions revealed that below this depth there was no separation in the relationship between temperature and salinity (Fig. 4). Therefore, below 150 m the underlying water at all sampling stations was essentially the same body of subantarctic source water.

Distribution and density of individual taxa

A total of 23 999 fishes from 107 taxa and 43 families were identified from the three years of sampling (Table 1). Myctophid fishes, totalling 42 species, dominated the catches and made up either 8 or 9 of the top 10 species by rank in each year (Table 2). The only non-myctophid taxon to figure consistently in the top ten

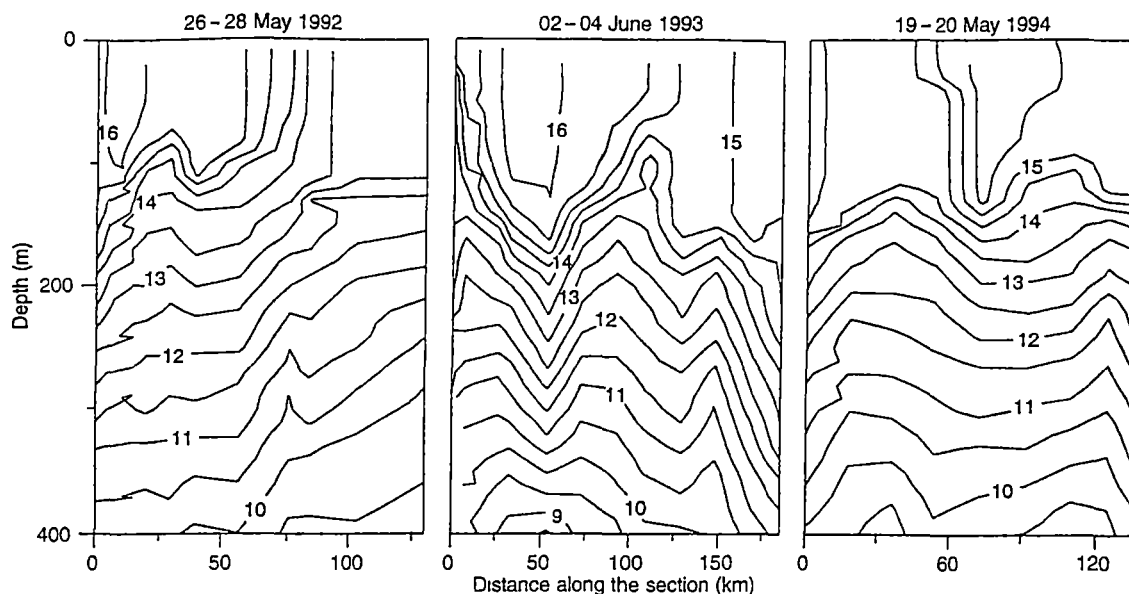


Fig. 3 Vertical temperature ($^{\circ}\text{C}$) structure from CTD casts to 400 m eastward along 42°S off eastern Tasmania, Australia, between 1992 and 1994

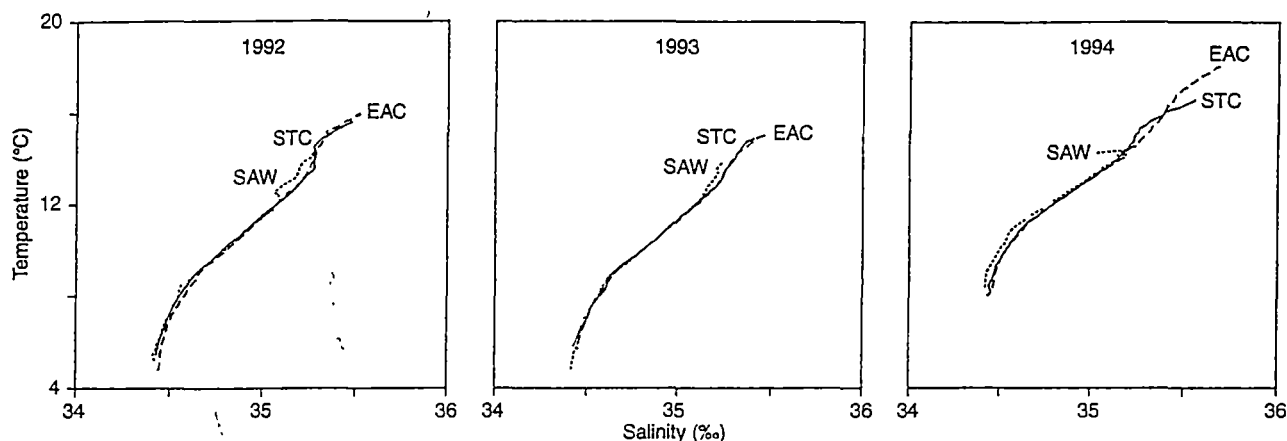


Fig. 4 Relationship between temperature and salinity in the three main water bodies off eastern Tasmania, Australia, between 1992 and 1994

ranking was the Stomiiformes genus *Vinciguerria*. During the three years, catches were small, with the maximum mean number of one individual species (*Diaphus danae*) in a year being merely $29.41 (\pm 11.56 \text{ SE})$ per 10^5 m^3 . Of the major groups, only the categories "all fishes", Myctophiformes, and Stomiiformes were caught in sufficient numbers for further analysis.

Of these three groups, only total Stomiiformes showed a significant difference between years; total Stomiiformes density was significantly lower in 1994 than in 1992 (Table 3, Fig. 5; Tukey's $q = 5.27$, $df = 46$, $p = 0.00$). No difference was found between years for

"all fishes" or for total myctophids. However, there were significant differences between years for some of the individual taxa within these groups, although no consistent pattern was detected (Table 3, Fig. 5). The density of *Diaphus danae* was significantly higher in 1994, whereas *Lampanyctus australis* and *Lampichthys procerus* were present in greater densities in 1993. In contrast, the density of *Vinciguerria* spp. was significantly higher in 1992.

No significant difference in the density of the main groups was found between areas (Table 3). However, the density of the most abundant stomiiform, *Vinciguerria* spp., was significantly higher in the EAC than in the SAW (Tukey's $q = 5.05$, $df = 46$, $p = 0.00$; Fig. 5). Similarly, although the density of total myctophids did not differ between areas, the density of four of the common species did. *Lampichthys procerus*

Table 1 Total number of individuals of each species identified from midwater trawls between 1992 and 1994 off eastern Tasmania, Australia (*new record for region) Taxa listed in taxonomic order (Eschmeyer 1990)

Species	1992	1993	1994	(Total)	Species	1992	1993	1994	(Total)
Anguilliformes					<i>Lampanyctus alatus</i>	9	5	26	(40)
Congridae					<i>Lampanyctus ater</i>	9	28	8	(45)
<i>Bassanago</i> spp	6	8	0	(14)	<i>Lampanyctus australis</i>	722	1 664	277	(2663)
Derichthyidae					<i>Lampanyctus festivus</i>	3	0	0	(3)
<i>Nessorhamphus ingolfianus</i>	0	5	0	(5)	<i>Lampanyctus intricatus</i>	2	31	0	(33)
Nemichthyidae					<i>Lampanyctus lepidolichnus</i>	46	299	46	(391)
<i>Atocettina</i> spp.	1	1	0	(2)	<i>Lampanyctus pusillus</i>	118	8	11	(137)
<i>Nemichthys curvirostris</i>	0	5	0	(5)	<i>Lampanyctus</i> sp. (H3977-01)	1	0	0	(1)
Leptocephalus	2	67	4	(143)	<i>Lamprochthys procerus</i>	706	1 782	116	(2604)
Salmoniformes					<i>Lobianchia doylei</i>	260	498	128	(886)
Bathylagidae	128	117	10	(255)	<i>Lowena interrupta</i> *	2	0	0	(2)
Stomiformes					<i>Metellectrona ventralis</i>	126	74	10	(210)
Opisthoproctidae	3	5	2	(10)	<i>Myctophum phenoxodes</i>	19	467	59	(545)
Platyroctidae					<i>Notoscoelus resplendens</i>	65	15	25	(105)
<i>Persparia kopua</i>	66	94	6	(166)	<i>Protomyctophum normani</i>	418	119	34	(571)
Stomidae	22	4	2	(28)	<i>Protomyctophum subparallelum</i>	1	0	0	(1)
Chauliodontidae					<i>Scopelogadus multipunctatus</i>	119	133	20	(272)
<i>Chauliodus sloani</i>	28	91	15	(134)	<i>Symbolophorus barnardi</i>	111	379	31	(521)
Astronesthidae					<i>Symbolophorus hoops</i>	19	14	2	(35)
<i>Astronesthes</i> spp.	2	12	0	(14)	Gadiformes				
<i>Neonesthes</i> spp.	0	2	0	(2)	Merlucciidae				
Idiacanthidae					<i>Lyconus</i> spp.	2	1	2	(5)
<i>Idiacanthus</i> spp.	15	31	3	(49)	Melanonidae				
Malacosteidae					<i>Melanonus</i> spp.	8	14	0	(22)
<i>Malacosteus niger</i>	0	1	0	(1)	Bregmacerotidae				
Melanostomidae					<i>Bregmaceros</i> sp	1	0	0	(1)
<i>Bathophilus</i> spp.	0	2	0	(2)	Macrouridae	0	5	0	(5)
<i>Leptostomus</i> sp	0	1	0	(1)	<i>Mesobius antipodum</i>	0	0	1	(1)
<i>Melanostomus</i> spp.	12	7	3	(22)	Lophiiformes				
<i>Trigonolampa muriceps</i> *	1	0	0	(1)	Ceratidae	3	0	0	(3)
Photichthyidae					<i>Cryptosarus couesi</i>	1	8	2	(11)
<i>Ichthyococcus olatus</i>	8	10	2	(20)	Onerodidae	3	6	0	(9)
<i>Photichthys argenteus</i>	105	144	54	(303)	Melanocetidae				
<i>Polymetme corythaeola</i>	1	22	2	(25)	<i>Melanocetus</i> spp	5	8	1	(14)
<i>Vinciguerria</i> spp.*	942	355	81	(1378)	Himantolophidae				
<i>Woodsia nonsuchae</i>	53	77	1	(131)	<i>Himantolophus appeli</i>	0	1	0	(1)
Gonostomatidae					Unidentified anglerfish	4	0	2	(6)
<i>Gonostoma</i> spp.	0	2	0	(2)	Beryciformes				
Sternoptychidae					Trachichthyidae				
<i>Argyropelecus aquas</i>	42	0	0	(42)	<i>Aulotrachichthys</i> sp	1	0	0	(1)
<i>Argyropelecus</i> spp	30	124	34	(188)	Diretmidae				
<i>Maurolagus muelleri</i>	4	29	5	(38)	<i>Diretmus argenteus</i>	2	78	16	(96)
<i>Polvipnus</i> spp	6	19	9	(34)	Anoplogasteridae				
<i>Sternoptyx diaphana</i>	5	5	0	(10)	<i>Anoplogaster cornuta</i>	3	1	0	(4)
<i>Valenciennellus tripunctulatus</i>	3	0	0	(3)	Melamphidae	10	47	5	(62)
Aulopiformes					Syngnathiformes				
Scopelarchidae	1	6	3	(10)	Macroramphosidae				
Notosudidae					<i>Macroramphosus scolopax</i>	16	1	0	(17)
<i>Scopelosaurus</i> spp	58	78	11	(147)	Scorpaeniformes				
Paralepididae	24	1	2	(27)	Scorpaenidae				
Evermannellidae	10	13	5	(28)	<i>Setarches</i> sp	0	0	1	(1)
Myctophiformes					Perciformes				
Myctophidae					Acropomatidae				
<i>Benthosema suborbitale</i>	21	123	30	(174)	<i>Howella sherboni</i>	102	103	16	(221)
<i>Bolinichthys nikolavi</i>	1	0	0	(1)	Bramidae				
<i>Ceratoscoelus warmingi</i>	389	168	169	(726)	<i>Brama brama</i>	1	1	0	(2)
<i>Diaphus brachycephalus</i> *	1	0	0	(1)	<i>Pterycombus petersi</i>	1	0	0	(1)
<i>Diaphus danae</i>	1708	1568	2032	(5308)	Carangidae	3	0	0	(3)
<i>Diaphus effulgens</i>	20	17	0	(37)	<i>Naurates ductor</i>	0	0	1	(1)
<i>Diaphus hudsoni</i>	414	511	132	(1057)	<i>Trachurus declivis</i>	0	0	3	(3)
<i>Diaphus meadi</i>	108	1	0	(109)	Chasmodontidae				
<i>Diaphus mollis</i>	2	3	0	(5)	<i>Kali</i> spp.	1	3	0	(4)
<i>Diaphus ostensfeldi</i>	12	28	5	(45)	Champsodontidae				
<i>Diaphus parri</i>	0	0	1	(1)	<i>Champsodon</i> spp	2	0	0	(2)
<i>Diaphus perspicillatus</i> *	0	0	3	(3)	Gempylidae				
<i>Diaphus termophilus</i>	78	154	43	(275)	<i>Paradiplosinus gracilis</i>	0	0	1	(1)
<i>Diaphus watasei</i>	0	0	2	(2)	<i>Thysites atun</i>	0	3	0	(3)
<i>Electrona pauciratra</i>	6	6	0	(12)	<i>Thysitoides marleyi</i>	0	0	1	(1)
<i>Electrona risso</i>	253	237	133	(623)	Nomeidae				
<i>Electrona subaspera</i>	90	0	0	(90)	<i>Cubiceps caeruleus</i>	0	0	1	(1)
<i>Gymnoscoelus pabilis</i>	7	2	0	(9)	Tetraodonidae				
<i>Hypogomphus hansen</i>	967	799	157	(1923)	<i>Tetiagonurus</i> spp.	1	21	25	(47)
<i>Hypogomphus hygoni</i>	0	0	1	(1)	Tetraodontiformes				
<i>Lampadena luminosa</i> *	0	0	1	(1)	Ostraciidae				
<i>Lampadena notialis</i>	21	20	0	(41)	<i>Lactoria diaphana</i>	0	0	1	(1)
<i>Lampanyctodes hectoris</i>	0	700	0	(700)					
					Total number of fishes	8672	11 492	3835	(23 999)
					Number of species	83	77	63	(107)

* See "Materials and methods – Laboratory analyses" for details of species structure

Table 2 Mean density (*D*, mean nos. 10⁻⁵ m⁻³), frequency of occurrence (*F*) and rank (*R*) as a function of year of overall top ten fish taxa off eastern Tasmania, Australia. Taxa listed in alphabetical order. Mean density and frequency of occurrence of three major groups are also listed

Species	1992				1993				1994			
	D	SE	F	(R)	D	SE	F	(R)	D	SE	F	(R)
All fishes	73.98	14.60	24		65.35	6.08	22		56.87	14.50	9	
Myctophiformes	57.13	11.93	24		56.12	5.98	22		51.87	13.74	9	
Stomiiformes	10.95	2.23	24		5.14	0.53	22		3.06	0.76	9	
<i>Ceratoscopelus warmingi</i>	3.29	1.19	15	(7)	0.89	0.23	18	(14)	2.57	2.07	5	(6)
<i>Diaphus danae</i>	13.62	3.42	23	(1)	8.58	1.22	22	(3)	29.41	11.56	9	(1)
<i>Diaphus hudsoni</i>	3.42	0.87	21	(6)	2.80	0.45	20	(5)	1.98	0.52	9	(4)
<i>Electrona risso</i>	2.06	0.42	21	(9)	1.31	0.33	20	(12)	1.90	0.89	8	(5)
<i>Hygophum hanseni</i>	8.70	3.75	22	(2)	4.46	0.79	21	(4)	2.42	0.69	8	(3)
<i>Lampanyctodes hectoris</i>	0.00	0.00	0	(85)	5.40	5.24	10	(6)	0.00	0.00	0	(65)
<i>Lampanyctus australis</i>	6.03	1.73	22	(4)	9.17	1.33	22	(2)	4.47	1.67	8	(2)
<i>Lampichthys procerus</i>	5.95	1.84	19	(5)	10.25	3.28	22	(1)	1.84	0.82	6	(8)
<i>Lobianchia dofleini</i>	2.25	0.61	18	(10)	2.63	0.56	20	(7)	1.92	1.05	6	(7)
<i>Vinciguerra</i> spp.	8.10	1.84	23	(3)	1.90	0.38	21	(10)	1.19	0.50	5	(10)

Table 3 Comparisons between years, areas and their interactions, of three major fish groups and top ten midwater fish species off eastern Tasmania, Australia, using ANOVA

Species	Year			Area			Year/area interaction		
	(df)	F	p	(df)	F	p	(df)	F	p
All fishes	(2)	0.54	NS	(2)	0.45	NS	(4)	0.39	NS
Myctophiformes	(2)	1.40	NS	(2)	0.41	NS	(4)	0.40	NS
Stomiiformes	(2)	6.08	0.01	(2)	2.78	NS	(4)	0.52	NS
<i>Ceratoscopelus warmingi</i>	(2)	2.11	NS	(2)	6.05	0.01	(4)	0.22	NS
<i>Diaphus danae</i>	(2)	3.13	0.05	(2)	3.60	0.04	(4)	0.93	NS
<i>Diaphus hudsoni</i>	(2)	0.93	NS	(2)	1.15	NS	(4)	1.48	NS
<i>Electrona risso</i>	(2)	0.24	NS	(2)	2.29	NS	(4)	2.48	0.06
<i>Hygophum hanseni</i>	(2)	0.85	NS	(2)	0.19	NS	(4)	1.48	NS
<i>Lampanyctodes hectoris</i>	(2)	1.68	NS	(2)	0.31	NS	(4)	0.46	NS
<i>Lampanyctus australis</i>	(2)	5.14	0.01	(2)	1.55	NS	(4)	1.32	NS
<i>Lampichthys procerus</i>	(2)	4.33	0.02	(2)	7.26	0.00	(4)	0.61	NS
<i>Lobianchia dofleini</i>	(2)	1.23	NS	(2)	3.42	0.04	(4)	0.87	NS
<i>Vinciguerra</i> spp	(2)	12.47	0.00	(2)	5.70	0.00	(4)	0.10	NS

was significantly more abundant in the SAW than in the EAC (Tukey's $q = 5.84$, $df = 48$, $p = 0.00$; Fig. 5). In contrast, the numbers of *Ceratoscopelus warmingi* and *Lobianchia dofleini* were significantly higher in the EAC than in the SAW (*C. warmingi*: Tukey's $q = 5.17$, $df = 48$, $p = 0.00$; *L. dofleini*: Tukey's $q = 3.88$, $df = 48$, $p = 0.04$; Fig. 5). Further, densities of *C. warmingi* were significantly higher in the EAC than in the STC (Tukey's $q = 2.04$, $df = 48$, $p = 0.04$; Fig. 5). *Diaphus danae* was present in significantly higher numbers in the STC than in the SAW (Tukey's $q = 4.65$, $df = 48$, $p = 0.03$; Fig. 5).

Depth distributions of individual taxa

Initially, we examined the top ten taxa in relation to year, area and depth for the two years where we sampled discrete depths (see "Materials and methods

- Sampling"). Of the taxa for which there was no interaction between year and depth (Table 4), *Ceratoscopelus warmingi* was concentrated in the upper 100 m of the water column. *Diaphus danae* and *Lampichthys procerus* were concentrated in the mid strata; whereas *Electrona risso* was present in highest concentrations at 400 to 300 m (Fig. 6).

Seven of the 13 taxa showed a significant interaction between year and depth stratum; these taxa were analysed by year separately (Table 5). In 1992, none of these taxa differed in numbers between depth strata, whereas in 1993 all taxa differed significantly in numbers with stratum (Table 5). In 1993, the "all fishes" group was concentrated in the mid (200 to 100 m) stratum, reflecting the dominance of the myctophids, which were also concentrated within this depth range (Fig. 6). Within the Myctophidae, *Hygophum hanseni* was more commonly found in the upper 100 m of the water column, whereas *Lampanyctus australis* and

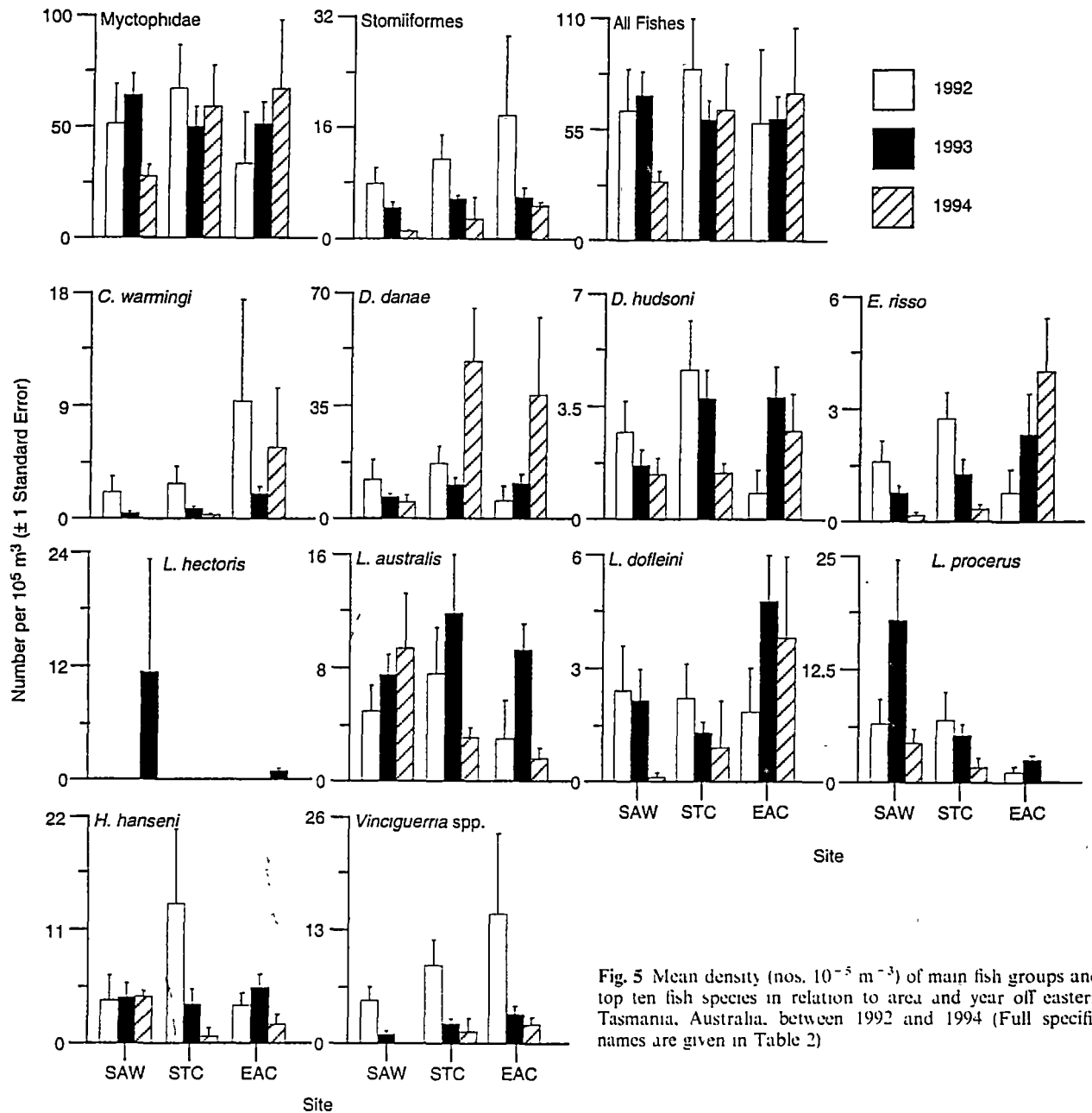


Fig. 5 Mean density (nos. 10^{-5} m^{-3}) of main fish groups and top ten fish species in relation to area and year off eastern Tasmania, Australia, between 1992 and 1994 (Full specific names are given in Table 2)

Lobianchia dofleini. were mainly concentrated in the mid strata (300 to 100 m). Total Stomiiformes, however, was concentrated more in the lower strata ($< 200 \text{ m}$) although *Vinciguerria* spp. was mainly concentrated in the mid strata (300 to 100 m).

Community differences

No outliers were detected in the community analysis by area. However, several outliers were detected in the analysis by depth. These outliers were caused by high

densities of some common species (e.g. *Lampanyctodes hectoris*) in some samples, reflecting the inherent patchiness of midwater fish, and therefore were not removed from the data set.

Community differences between areas

The species composition of the SAW was significantly different from both the STC and EAC. No difference was found between the STC and EAC (Table 6). The discriminant-function plot showed the 95% confidence

Table 4 Summary of between-year and between-depth-stratum comparisons of midwater fishes off eastern Tasmania, Australia (using ANOVA) for which there were no year/stratum interactions

Species	Effect								
	Year			Stratum			Year/stratum		
	(df)	F	p	(df)	F	p	(df)	F	p
<i>Ceratoscopelus warmingi</i>	(1)	0.13	NS	(3)	3.87	0.01	(3)	0.90	NS
<i>Diaphus danae</i>	(1)	3.70	0.06	(3)	4.19	0.01	(3)	0.66	NS
<i>Diaphus hudsoni</i>	(1)	6.05	0.02	(3)	1.25	NS	(3)	1.40	NS
<i>Electrona risso</i>	(1)	0.47	NS	(3)	6.37	0.00	(3)	1.09	NS
<i>Lampanyctodes hectoris</i>	(1)	3.49	0.06	(3)	0.56	NS	(3)	0.56	NS
<i>Lampichthys procerus</i>	(1)	8.39	0.00	(3)	4.15	0.01	(3)	2.07	NS

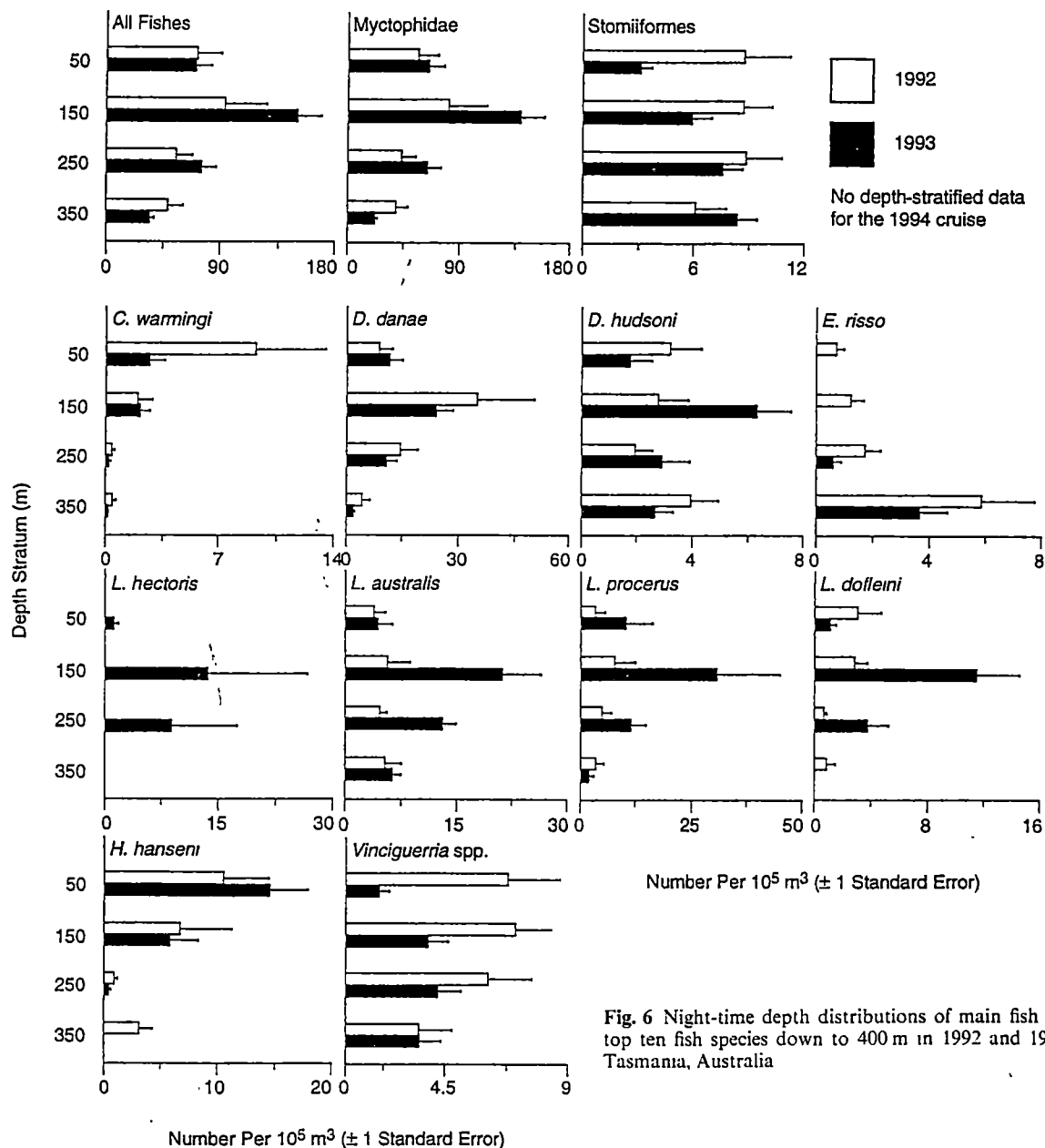


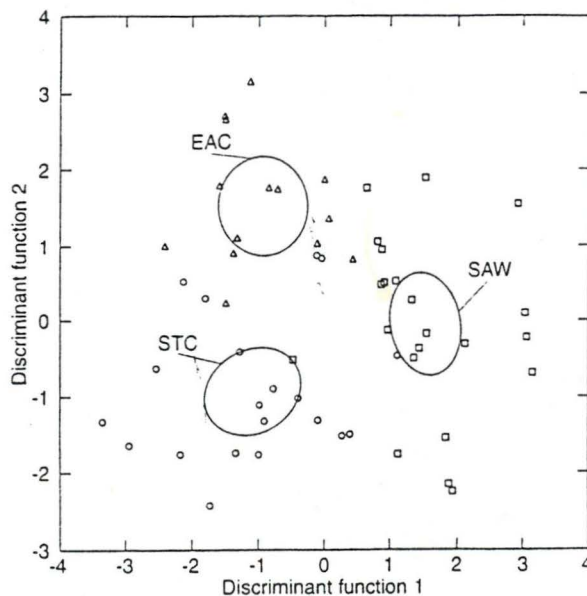
Fig. 6 Night-time depth distributions of main fish groupings and top ten fish species down to 400 m in 1992 and 1993, off eastern Tasmania, Australia

Table 5 Summary of between-depth comparisons of midwater fishes that showed a significant year/stratum interaction

Species	1992			1993		
	(df)	F	p	(df)	F	p
All fishes	(3)	0.05	NS	(3)	12.98	0.00
Myctophiformes	(3)	0.07	NS	(3)	18.24	0.00
Stomiiformes	(3)	0.75	NS	(3)	6.26	0.00
<i>Hygophum hanseni</i>	(3)	2.45	NS	(3)	14.26	0.00
<i>Lampanyctus australis</i>	(3)	0.72	NS	(3)	12.00	0.00
<i>Lobianchia dofleini</i>	(3)	1.63	NS	(3)	23.29	0.00
<i>Vinciguerria</i> spp.	(3)	1.75	NS	(3)	2.75	0.05

Table 6 Summary of pairwise comparisons between areas (SAW subantarctic water; STC subtropical convergence; EAC East Australia Current) using Roy's greatest characteristic root (*gcr*) (Bird and Hadzi-Pavlovic 1983). Contrast statistic = $\theta_1/1 - \theta_1$, where θ_1 = Roy's *gcr*. Critical *gcr* = 1.058 (* $p < 0.05$)

Comparison		Contrast statistic	p
a	b		
SAW	STC	1.53	*
SAW	EAC	1.34	*
EAC	STC	0.91	NS

**Fig. 7** Discriminant-function plot of fish-community data off eastern Tasmania, Australia, for all years combined, with 95% confidence ellipses around centroid of each area category (□ SAW; ○ STC; △ EAC)

interval about the centroids of the SAW, STC and EAC groups to be distinct (Fig. 7). However, STC and EAC groups varied only in the second discriminant function, whereas the SAW group differed in both axes (Fig. 7). A test of residual roots showed a reliable relationship between groups and predictors ($\chi^2 = 72.21$,

$df = 32$, $p < 0.001$) which remained strong in the second function ($\chi^2 = 28.74$, $df = 15$, $p < 0.05$). The two discriminant functions accounted for 57 and 43%, of the between group variability, respectively.

Examination of the canonical correlations revealed that *Lampichthys procerus* was positively correlated in the first discriminant function, whereas *Vinciguerria* spp. were negatively correlated (Table 7). The group means showed that the density of *L. procerus* was higher in the SAW than in the STC or EAC, whereas *Vinciguerria* spp. density was lower in the SAW (Table 8). In the second discriminant function, *Ceratoscopelus warmingi* and *Lobianchia dofleini* were positively correlated (Table 7), whereas *Lampichthys procerus* was negatively correlated, signifying that the density of *C. warmingi* and *Lobianchia dofleini* was greater in the EAC (Table 8).

Community differences between depths

The species composition of the four depth strata were all significantly different from each another (Table 9). The discriminant-function plot (Fig. 8) showed that the 95% confidence interval about the centroid of the 50 m stratum was separated from those of all other strata on both axes. The 150 and 250 m strata were separated in the first dimension, and those of the 250 and 350 m strata were separated in the second dimension. A test of residual roots showed a reliable relationship between groups and predictors ($\chi^2 = 192.85$, $df = 57$, $p < 0.001$) which remained strong after the removal of the first function ($\chi^2 = 93.72$, $df = 36$, $p < 0.001$). The first discriminant function explained 48% of the variation while the second explained 39%.

Canonical correlations of the first discriminant function showed that *Diaphus termophilus* and *Electrona risso* were positively correlated with the first axis (Table 7); *Ceratoscopelus warmingi*, *Hygophum hanseni*, *Myctophum phengodes* and *Symbolophorus barnardi* were negatively correlated. The density of the positively correlated species increased with increasing depth, whereas the density of the negatively correlated species decreased with increasing depth (Table 10). Canonical correlations of the second discriminant function showed that *E. risso* was positively correlated, whereas *Diaphus danae*, *Lampanyctus australis*, *L. lepidolichnus*, *Lampichthys procerus*, *Lobianchia dofleini*, and *Scopelopsis multipunctatus* were negatively correlated (Table 7). The negatively correlated species were those with greatest densities in the 150 and 250 m depth strata (Table 10).

Community analysis of area and depth

Finally, we pooled the depth data into shallow (two uppermost strata) and deep (two bottom strata) for

Table 7 Canonical correlations (CC) of first two discriminant functions from discriminant-function analyses of area differences and depth-stratum differences off eastern Tasmania, Australia (– not included in analyses)

Species	Area analysis		Depth analysis	
	CC 1	CC 2	CC 1	CC 2
<i>Benthosema suborbitale</i>	–	–	– 0.24	– 0.12
<i>Ceratoscopelus warmingi</i>	– 0.24	0.32	– 0.44	– 0.02
<i>Diaphus danae</i>	– 0.23	– 0.05	– 0.12	– 0.50
<i>Diaphus hudsoni</i>	– 0.24	– 0.14	0.10	– 0.12
<i>Diaphus termophilus</i>	– 0.21	0.10	0.47	0.00
<i>Electrona risso</i>	– 0.24	0.06	0.42	0.35
<i>Howella sherboni</i>	–	–	0.20	– 0.24
<i>Hygophum hanseni</i>	– 0.08	– 0.04	– 0.45	0.14
<i>Lampanyctus australis</i>	0.02	– 0.17	0.29	– 0.33
<i>Lampanyctus lepidolichnus</i>	– 0.02	0.07	0.10	– 0.42
<i>Lamprolaima procerus</i>	0.31	– 0.39	0.03	– 0.53
<i>Lobianchia doylei</i>	– 0.14	0.33	– 0.18	– 0.60
<i>Metellectrona ventralis</i>	–	–	0.05	– 0.11
<i>Myctophum phengodes</i>	0.16	0.10	– 0.34	– 0.06
<i>Photichthys argenteus</i>	0.14	0.12	–	–
<i>Protomyctophum normani</i>	0.15	– 0.18	0.07	– 0.18
<i>Scopelopsis multipunctatus</i>	– 0.08	0.27	– 0.09	– 0.33
<i>Symbolophorus barnardi</i>	– 0.13	– 0.05	– 0.39	– 0.20
Unidentified myctophids	–	–	0.09	– 0.02
<i>Vinciguerrria</i> spp.	– 0.31	– 0.02	0.01	– 0.29

Table 8 Mean density (nos. 10⁻³m⁻³) of taxa used in analyses of community difference as a function of area (abbreviations as in Table 6)

Species	SAW		STC		EAC	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Bathylagidae	0.83	0.23	0.62	0.23	0.79	0.20
<i>Ceratoscopelus warmingi</i>	0.99	0.54	1.88	0.85	4.80	2.04
<i>Diaphus danae</i>	8.43	2.45	18.20	4.10	17.77	7.56
<i>Diaphus hudsoni</i>	2.03	0.46	4.04	0.96	2.77	0.61
<i>Diaphus termophilus</i>	0.51	0.15	0.85	0.20	0.91	0.18
<i>Electrona risso</i>	1.00	0.27	2.06	0.46	2.47	0.69
<i>Hygophum hanseni</i>	4.25	1.12	9.27	4.44	3.84	0.78
<i>Lampanyctus lepidolichnus</i>	0.88	0.24	0.84	0.24	1.14	0.43
<i>Lamprolaima procerus</i>	11.41	3.32	5.82	1.92	1.35	0.41
<i>Lampanyctus australis</i>	6.68	1.08	8.44	2.27	5.44	1.41
Larval fish	0.31	0.12	1.22	0.53	0.74	0.36
<i>Lobianchia doylei</i>	1.97	0.61	1.81	0.54	3.80	0.84
<i>Myctophum phengodes</i>	1.99	0.89	0.71	0.43	0.82	0.35
<i>Photichthys argenteus</i>	0.99	0.20	0.63	0.15	0.90	0.29
<i>Protomyctophum normani</i>	2.85	1.19	1.31	0.51	0.43	0.31
<i>Scopelopsis multipunctatus</i>	0.80	0.43	0.59	0.22	1.17	0.30
<i>Symbolophorus barnardi</i>	1.20	0.37	1.50	0.32	1.26	0.27
<i>Vinciguerrria</i> spp.	2.40	0.76	6.11	1.90	5.53	2.23

samples from the three water bodies to examine the effect of depth on area. None of the deep groups differed significantly between areas, but all were significantly different from the shallow groups (Table 11, Fig. 9). Furthermore, the shallow EAC group was significantly different in all group comparisons bar that with the shallow STC. These results indicated that not only were there separate shallow and deep communities, but also that the fishes of the shallow EAC group formed a distinct community.

Discussion

Individual species distributions

Horizontal distributions

None of the ten most abundant species were completely absent from any one area. However, five taxa did show significant differences in density between areas:

Table 9 Summary of pairwise comparisons between depth strata using Roy's greatest characteristic root (qcr). Contrast statistic = $\theta_{1/1} - \theta_1$, where θ_1 = Roy's qcr . Critical $qcr = 0.339$ (* $p < 0.05$)

Comparison		Contrast statistic	J
a	b		
50	150	0.62	*
50	250	0.91	*
50	350	0.85	*
150	250	0.41	*
150	350	0.84	*
250	350	0.35	*

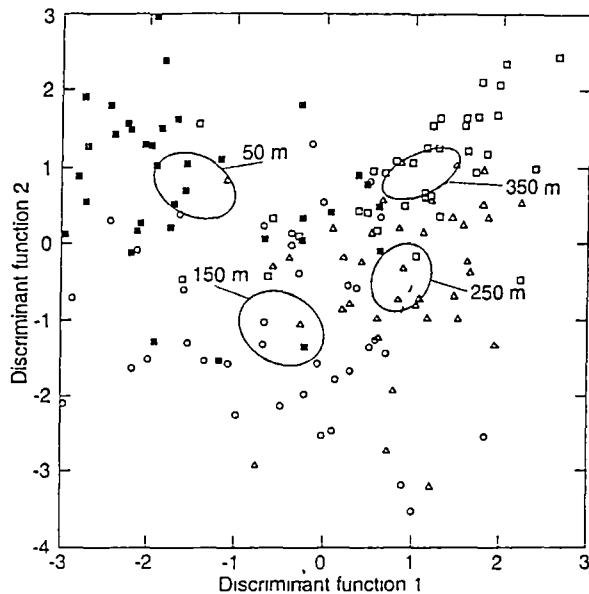


Fig. 8 Discriminant-function plot of fish-community data off eastern Tasmania, Australia, for 1992 and 1993 combined, with 95% confidence ellipses around centroid of each depth category (■ 50 m; ○ 150 m; △ 250 m; □ 350 m)

Ceratoscopelus warmingi, *Lobianchia dofleini*, *Vinciguerria* spp., *Diaphus danae*, and *Lampichthys procerus*. The first three species were found in greater density in the warmer waters of the EAC. These three have either tropical or subtropical distributions (Brandt 1981; Hulley 1981, 1986). *D. danae*, which is usually found in waters $< 16^{\circ}\text{C}$ (Brandt 1981), was most abundant in the STC. The greater density of *L. procerus* in the SAW supports the observations that this species is usually associated with the southern boundary of the subtropical convergence (Hulley 1981, 1986).

There were no clear patterns of distribution among the remaining species: *Diaphus hudsoni*, *Hygophum hanseni*, *Lampanyctus australis* and *Electrona risso*. The first three species are generally found elsewhere in association with the STC (e.g. off South Africa), but are also

found in higher and lower latitudes (Nafpaktitis and Nafpaktitis 1969; Hulley 1986). Although not significant, there was a trend for greater numbers of *E. risso*, [which is generally regarded as a tropical species (Nafpaktitis et al. 1977; Hulley 1986)], in the EAC. The importance of *Lampanyctodes hectoris* in 1993 was due largely to one large catch taken over the shelf break. It was rarely taken offshore. The close association of this species with the continental slope in temperate waters has previously been reported from southern African and Australian waters (Hulley 1986; Young and Blaber 1986; May and Blaber 1989).

Depth distributions

Although similar, the two years of depth data displayed some important differences. The 1993 data showed more distinct patterns of species density with depth. As the same opening/closing net was used in both years it is likely that the differences were real. The reason for these differences, however, is not clear, although there was a waxing moon during the 1992 cruise and this may have affected the distributions of some species. Clarke (1973) reported deeper distributions of the lanternfish *Benthosema suborbitale* during periods of full moon.

Overall, lanternfish were concentrated in the upper depth strata. This result agrees with earlier accounts of the vertical distribution of myctophids in the northern hemisphere, where there is a general movement from below 500 m by day to above 250 m depth at night (Karnella 1987). Most of the abundant species were distributed over the 400 m depth range we sampled, with peaks of abundance in, but not limited to, a particular stratum. These broad distributions may be the result of staggered migrations of individuals within a species. For example, Pearcy and Laurs (1966) found that not all individuals in a population of the lanternfish *Stenobrachius leucopsarus* migrated to the surface every night. We also noted that *Diaphus danae* juveniles were closer to the surface at night than adults (Young unpublished data). Nevertheless, there were some species with narrow depth distributions. *Ceratoscopelus warmingi* and *Hygophum hanseni* were concentrated in the upper 100 m, which agrees with earlier accounts of their vertical distribution (Bekker and Borodulina 1968; McGinnis 1982). In contrast, *Electrona risso* was most abundant below 300 m. This is apparently not the limit of its distribution, as this species is abundant below 400 m (Nafpaktitis et al. 1977).

Some of the distributions we found were different from previous studies. For example, *Lampanyctus australis* and *Lampichthys procerus*, which had peaks of density between 100 and 200 m, were reported below 400 m during the night by Hulley (1981). *Diaphus temophilus*, which was collected in higher numbers in our deeper samples, is recorded as being most abundant at

Table 10 Mean density (nos. 10^{-5}m^{-3}) of taxa used in analyses of community differences as a function of depth stratum

Species	50 m		150 m		250 m		350 m	
	\bar{x}	(SE)	\bar{x}	(SE)	\bar{x}	(SE)	\bar{x}	(SE)
<i>Benthoosema suborbitale</i>	1.54	(0.63)	1.97	(0.37)	0.30	(0.17)	0.11	(0.05)
<i>Ceratoscopelus warmingi</i>	6.29	(2.38)	2.11	(0.56)	0.23	(0.10)	0.24	(0.13)
<i>Diaphus termophilus</i>	0.04	(0.03)	2.56	(0.20)	1.49	(0.37)	1.40	(0.28)
<i>Diaphus danae</i>	8.15	(2.25)	30.56	(8.18)	11.64	(2.98)	2.88	(0.99)
<i>Diaphus hudsoni</i>	2.43	(0.74)	4.87	(0.93)	2.03	(0.41)	3.49	(0.61)
<i>Electrona risso</i>	0.37	(0.15)	0.61	(0.25)	1.23	(0.33)	5.01	(1.09)
<i>Howella sherboni</i>	0.33	(0.23)	0.82	(0.22)	1.41	(0.34)	0.68	(0.28)
<i>Hygophum hanseni</i>	12.77	(2.72)	6.56	(2.69)	0.54	(0.21)	1.52	(0.64)
<i>Lamprolaima procerus</i>	3.75	(2.22)	17.91	(8.18)	6.99	(1.73)	2.27	(0.94)
<i>Lobianchia doylei</i>	2.00	(0.91)	7.68	(1.89)	1.60	(0.60)	0.42	(0.31)
<i>Lampanyctus australis</i>	3.17	(1.10)	14.34	(3.56)	8.69	(1.25)	6.33	(1.27)
<i>Lampanyctus lepidolichnus</i>	0.30	(0.18)	2.22	(0.55)	2.49	(1.00)	0.40	(0.14)
<i>Metellectrona ventralis</i>	0.52	(0.32)	1.72	(0.90)	0.68	(0.31)	0.70	(0.24)
<i>Myctophum phlegodes</i>	6.15	(2.70)	3.44	(1.56)	0.37	(0.19)	0.06	(0.04)
<i>Protomyctophum normani</i>	0.33	(0.14)	3.11	(1.64)	3.09	(2.16)	1.99	(1.36)
<i>Scopelopsis multipunctatus</i>	1.09	(0.84)	2.14	(0.71)	0.58	(0.21)	0.21	(0.13)
<i>Symbolophorus barnardi</i>	2.55	(0.44)	3.32	(0.72)	0.88	(0.27)	0.44	(0.16)
Unidentified myctophids	0.67	(0.28)	0.73	(0.24)	1.19	(0.43)	0.91	(0.33)
<i>Vinciguerria</i> spp.	3.76	(1.17)	5.25	(0.88)	4.57	(0.99)	3.11	(0.83)

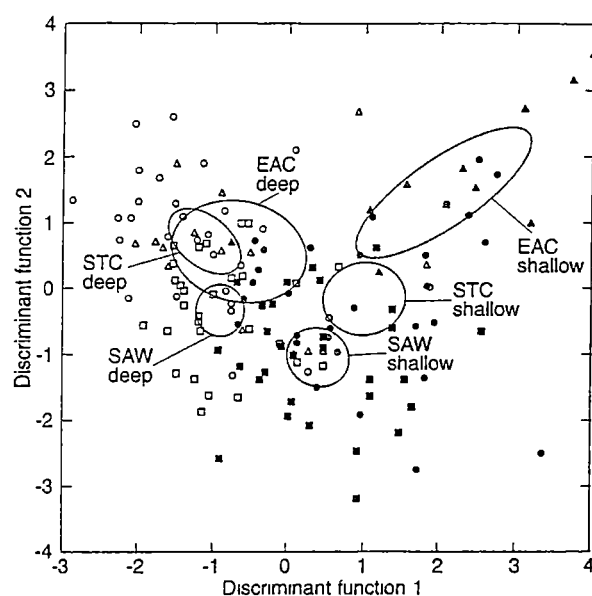
Table 11 Summary of pairwise comparisons between area/depth groups using Roy's greatest characteristic root (*gcr*). Contrast statistic = $\theta_1/1 - \theta_1$, where θ_1 = Roy's *gcr*. Critical *gcr* = 1.058 (* $p < 0.05$)

Comparison		Contrast statistic <i>p</i>	
a	b		
SAW shallow	SAW deep	0.42	NS
	STC shallow	0.32	NS
	deep	0.62	*
	EAC shallow	0.61	*
	deep	0.31	NS
deep	STC shallow	0.49	*
	deep	0.26	NS
	EAC shallow	0.81	*
	deep	0.19	NS
STC shallow	STC deep	0.66	*
	EAC shallow	0.35	NS
	deep	0.33	NS
deep	EAC shallow	0.73	*
	deep	0.09	NS
EAC deep	EAC shallow	0.45	*

100 m in the northern hemisphere (Nafpaktitis et al. 1977).

Community analyses

Analysis of the community structure showed that the EAC differed from the SAW but not from the STC. This result appeared to be driven by the community inhabiting the upper layers of the EAC. Earlier studies of warm-core eddies shed from the EAC have shown

**Fig. 9** Discriminant-function plot of fish-community data off eastern Tasmania, Australia, for 1992 and 1993 combined, with 95% confidence ellipses around centroid of each depth/area category (■ SAW shallow; □ SAW deep; ● STC shallow; ○ STC deep; ▲ EAC shallow; △ EAC deep)

that many faunal communities – including fish (e.g. Brandt 1981) – differ inside and outside such eddies (see also Griffiths and Wadley 1986). These eddies trap species of tropical origin and, although there is some mixing with Tasman Sea species, they remain reasonably distinct from the surrounding water. Our data indicate that although the thin EAC layer off eastern

Tasmania is the southernmost extension of the main East Australia Current it is still, in some ways, distinct from the surrounding waters. However, we could distinguish little difference in either abundance or community structure between the STC and the surrounding water masses. This contrasts with the data of Robertson et al. (1978), who found clear correspondence between mesopelagic communities and water masses associated with the subtropical convergence off the east coast of New Zealand. The STC in their region is cooler than off Tasmania, and the layer of warm water at the surface is approximately twice as deep (170 to 300 m). In our study, the dominance of the underlying subantarctic water, coupled with the relative broadness of the STC and the weak gradient in sea-surface temperature appeared to minimise the differences between even widely separated sampling stations. This is particularly true of the STC and EAC areas, which differed only in the depth of the overlying EAC water.

That there were few differences in density of individual or grouped fish taxa in the area of the subtropical convergence contrasts with the situation reported for many other marine taxa, including fishes, in similar areas. For example, in reviews of animals associated with fronts, herbivorous zooplankton, shoaling fishes, seabirds and even whales have been reported in greater abundance in, or near, fronts (Olson and Backus 1985; Sournia 1994). Of particular interest to the present study is the fact that several tuna species have also been reported in association with fronts (Shingu 1967; Uda 1973; Laurs et al. 1984; Fiedler and Bernard 1987).

Secondary circulation processes in frontal regions generally lead to enhanced biological activity, increasing production of phytoplankton and herbivorous zooplankton (Vidau et al. 1994). Larger, more motile marine animals are then believed to be attracted by the more abundant supply of prey (Olson and Backus 1985; Sournia 1994). However, the lack of strong thermal gradients in the study region and the thinness of the overlying EAC water appear to have reduced the horizontal and vertical scale of mixing, limiting secondary circulation and the resulting productivity. In a parallel study (Young et al. 1996), we were unable to find any evidence of enhanced zooplankton abundance in the frontal region. That the parallel study was completed in autumn/winter may also have affected the patterns we observed. Light limitation and an increase in the depth of the mixed layer during winter can combine to limit productivity along fronts (e.g. Pingree et al. 1976). However, Pakhomov et al. (1994) found that in winter off southern Africa the subtropical convergence contained a higher biomass than the surrounding waters. Of note was that in their case the difference in surface temperature between the north and the south of the front was $\sim 10^{\circ}\text{C}$ in $\sim 1^{\circ}$ of latitude. This gradient is more than twice the difference we found off Tasmania, indicating that production may be closely linked to the intensity of the front.

Interannual variation in fish distributions

The overall density of fish in the "all fishes" and Myctophiformes groups remained similar across all three years, although the Stomiiformes were present in greatest densities in 1992, due largely to variations in the numbers of *Vinciguerria* spp. The relative stability of fish numbers over the 3 yr study contrasted with that found for other zooplankton and micronekton groups (Young et al. 1996). Specifically, there was a progressive increase in zooplankton and micronekton biomass across the three years, largely driven by an increase in gelatinous zooplankton. The reason for this stability may be related to the fact that most of the species captured are only temporary night-time residents in the upper layers. By day, most are found below 400 m in the more stable subantarctic and Antarctic intermediate water. Certainly, the temperature/salinity relationships for the three years for waters below $\sim 12^{\circ}\text{C}$ are very similar.

Relationship to tuna distributions

Roger (1994) conceded that, with existing techniques, it was not possible to directly estimate the prey of tuna. Net collections fail to adequately sample the faster micronekton species. However, he showed that by sampling the prey of the tuna prey, correlations between productive plankton areas and tuna distributions could be made. It could be argued that the present study, by concentrating on midwater fishes (in particular myctophids), may not have adequately assessed the potential prey of the tunas. However, Auster et al. (1992) observed that myctophid fishes were generally associated with other pelagic fauna, many of which were prey of tuna. In the present study we were unable to distinguish an obvious area offshore that might attract larger predators. However, when we examined the composition and biomass of the inshore shelf region we identified significantly higher levels of suitable prey (Young et al. 1996). We suggest, therefore, that the STC is not, as some frontal areas appear to be, an area of increased abundance of micronekton. Moreover, its species composition is not significantly different from that of surrounding waters, its fauna being very similar to that of the EAC.

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PART B

ECOLOGICAL STUDIES

CHAPTER 5

**Reproductive biology of three species of midwater fishes associated
with the continental slope of eastern Tasmania, Australia.**

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Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia

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Abstract

The reproductive biology of *Lampanyctodes hectoris* (Günther, 1876), *Maurolicus muelleri* (Gmelin, 1789) and *Diaphus danae* Tåning, 1932, from continental-slope waters of eastern Tasmania, was examined between April 1984 and June 1985. *L. hectoris* spawned in winter and *M. muelleri* spawned from late winter to early summer. Apart from one ripe male, no reproductive activity was detected in *D. danae*; this species may be an expatriate in these waters. Fecundity was positively correlated with standard length in *L. hectoris*, but not in *M. muelleri*. The ratio of females to males increased with length in all three species. The spermatozoa of *L. hectoris* and *D. danae* are atypical of vertebrates and have no tail.

Introduction

Information on the reproductive biology of myctophid and stomiatoid fishes is limited and few comparative data are available. Reproductive studies have concentrated on either macroscopic staging of gonads (Paxton, 1967; Clarke, 1973; Badcock and Merrett, 1976; Karnella and Gibbs, 1977; Robertson, 1977; Gjosaeter, 1981a) or sizing of eggs (Halliday, 1970; Smoker and Percy, 1970; Pertseva-Ostroumova, 1973; Clarke, 1982). Few histological studies have been attempted (O'Day and Nafpaktitis, 1967; Zurbrigg and Scott, 1972) and none, to our knowledge, have examined seasonal changes in gonad maturity.

Lampanyctodes hectoris (Myctophidae), *Maurolicus muelleri* (Sternoptychidae), and *Diaphus danae* (Myctophidae) are the most abundant midwater fishes on the upper continental slope of eastern Tasmania (Young and Blaber, 1986). Midwater fishes, particularly *L. hectoris*, are the main diet of many slope fishes in these waters (Blaber and Bulman, 1987); however, a seasonal cycle in the abundance of these fishes has been reported (J. May,

personal communication). To understand the basis for this seasonality, the reproductive biology of these species was examined. Aspects of the reproductive biology of *M. muelleri* in eastern Australian waters were studied by Clarke (1982), but little has been reported on *L. hectoris* (Robertson, 1977, Crawford, 1980, Cruickshank, 1983) and nothing on *D. danae*.

Ripe *Lampanyctodes hectoris*, together with planktonic eggs, have been found off New Zealand during August (late winter) (Robertson, 1977). Larvae of *L. hectoris* have been taken off South Africa between August and November (Ahlstrom *et al.*, 1976). The principal spawning season of *Maurolicus muelleri* is between late winter and spring off eastern Australia (Clarke, 1982), coinciding with increased plankton production in the area. In New Zealand waters the main spawning period occurs later, in spring and summer (Robertson, 1976). No reproductive data are available for *Diaphus danae*.

This paper examines seasonal changes in the reproductive biology of each species, using gonad histology and gonadosomatic indices. It presents data on fecundity and sex ratios and provides a description of the mature spermatozoa of *Lampanyctodes hectoris*.

Materials and methods

Midwater fishes were collected at two-monthly intervals between April 1984 and June 1985 over the upper continental slope, 12 nautical miles east of Maria Island, Tasmania (42°39'S; 148°28'E). Sampling details are given in Young and Blaber (1986). The three most abundant midwater species, *Lampanyctodes hectoris* (Günther, 1876), *Maurolicus muelleri* (Gmelin, 1789), and *Diaphus danae* Tåning, 1932, were selected for reproductive examination. A size range of each species collected on each cruise was preserved in Bouin's fluid (Hale, 1958) and later transferred to 70% alcohol in the laboratory. Additional samples, preserved in 10% formalin, were taken for determination

Table 1. Criteria used for staging gonads of midwater fishes studied

Stage	Histology	
	Females	Males
(1) Immature	oogonia present	spermatogonia and some primary spermatocytes
(2) Resting/developing	mainly (> 50% of all egg types) previtellogenic oocytes; some oogonia	few spermatids; primary and secondary spermatocytes
(3) Maturing	mainly non-staining yolk; some yolk precursors	mainly spermatids and secondary spermatocytes
(4) Ripe	mainly red-staining yolk, some nonstaining yolk	mainly spermatozoa; some spermatids
(5) Ripe-running	homogeneous yolk, development complete	gonad all spermatozoa
(6) Spent-resting	atresion of ripe oocytes plus previtellogenic oocytes	–

of fecundity. Profiles of water temperature and salinity were taken over the study area on each cruise from standard hydrocasts to 400 m.

In the laboratory, fish were measured (standard length, SL, ± 0.5 mm) and weighed (± 0.001 g), and the gonads were removed and weighed (± 0.001 g). Gonads were embedded in paraffin wax, sectioned at $8\ \mu\text{m}$ and stained with haematoxylin and eosin (McManus and Mowry, 1960). Gonad maturation was classified according to Dipper and Pullin (1979) for females, and Davis (1977) and Cyrus and Blaber (1984) for males. Each gonad was staged, based on the relative amounts of developmental cells (Table 1).

No macroscopic staging was attempted because of the lack of obvious gonad differentiation in all but ripe fish. The fecundity of *Lampanyctodes hectoris* was established from oocytes larger than 0.30 mm. These were translucent to opaque, and distinguishable from smaller, transparent oocytes. In *Maurolicus muelleri*, fecundity was estimated from the number of enlarged, yolked oocytes (> 0.35 mm: Clarke, 1982) which were easily distinguishable from smaller, less developed ova. Because of an apparent bimodality in mature egg size in *L. hectoris* and *M. muelleri*, random samples of approximately 100 eggs were measured from ripe fish to determine whether there was evidence for multiple spawning. Scanning electron micrographs were taken of mature spermatozoa of *L. hectoris* after etching with HCl and gold-plating.

Data analysis

Seasonal variations in gonad maturation stage of females and males were compared, using analysis of variance. If a significant difference between months was found, pair-wise *t*-tests were used to test which months were significantly different. Gonadosomatic indices (GSI) were calculated as the ratio of gonad wet weight to total fish wet weight, expressed as a percentage. The GSI data were transformed to logarithms, as the samples from the populations had unequal variances. Seasonal variations in GSI values of females and males were examined, using either analysis of covariance (ANCOVA) or analysis of variance.

An ANCOVA was used if a regression of log (GSI) on log (SL), fitted separately to the fishes from each cruise, accounted for a significantly greater amount of variation than fitting only mean GSI values. Otherwise, an analysis of variance was used. Pair-wise *t*-tests were again used to identify months that were significantly different. As gonad maturation stage was not a continuous variable in *Lampanyctodes hectoris* and *Maurolicus muelleri*, the correlation between gonadosomatic index and gonad maturation stage was examined using the non-parametric Spearman rank correlation (r_s) test (Zar, 1984). Individuals were sexed from histological examinations, as there was no readily identifiable sexual dimorphism in the three species examined. Differences in sex ratios between cruises and with size were statistically tested using chi-squared goodness of fit.

Results

Physical environment

Mean sea-surface temperature ranged from 12.1°C in October to 18.5°C in the following April (Fig. 1), following the annual influx of surface tropical East Australian Current water to the prevailing modified subantarctic water (Harris *et al.*, in press). Temperatures at a depth of 200 m remained between 11.6° and 13.5°C throughout the year. Surface salinity values mirrored the temperature changes, with lowest salinities in October and December 1984 and highest in February and March 1985.

Reproduction

A total of 454 fish were examined. Table 2 gives the size range, sex and number of individuals examined from each sampling period.

Lampanyctodes hectoris

Seasonal changes in gonad development and gonadosomatic index. Ripe females of *Lampanyctodes hectoris* were usually greater than 55 mm SL, although one individual was ripe-

Table 2. *Lampanyctodes hectoris*, *Maurollicus muelleri* and *Diaphus danae*. Size range (standard length, SL), sex and number of individuals whose gonads were examined from off Maria Island between April 1984 and June 1985. —: absent

Month	<i>L. hectoris</i>			<i>M. muelleri</i>			<i>D. danae</i>		
	SL (mm)	Nos. of:		SL (mm)	Nos. of:		SL (mm)	Nos. of:	
		♀	♂		♀	♂		♀	♂
1984									
April	42–65	20	—	34–49	6	—	—	—	—
June	38–64	22	24	34–52	13	5	38–51	4	—
August	32–66	25	17	34–41	7	2	39–50	11	—
October	50–66	13	6	39–51	11	12	62–96	3	17
December	31–72	16	3	43–54	17	13	66–115	20	12
1985									
February	55–71	12	1	35–53	22	1	70–109	4	7
March	33–72	17	6	34–53	19	3	80–111	—	4
June	36–60	20	—	—	—	10	66–107	23	6
Total nos.		145	57		95	46		65	46
Sex ratio (♀:♂)		2.16:1			2.64:1			1.64:1	

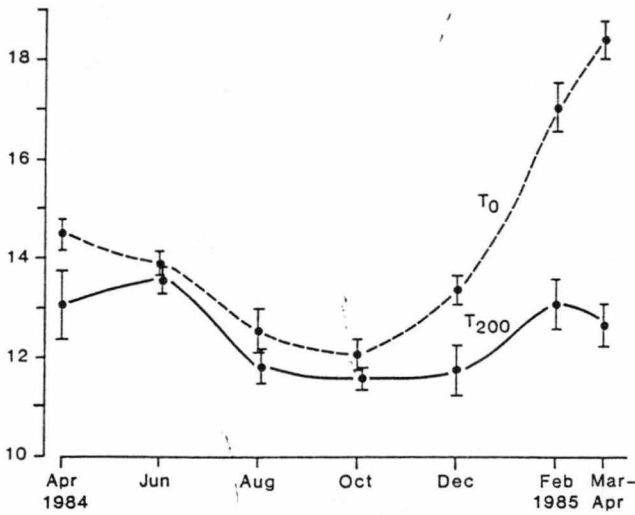


Fig. 1. Mean sea-surface temperatures (T_0) and mean temperatures at 200 m (T_{200}) depth over continental slope, east of Maria Island between April 1984 and March/April 1985. Bars define 95% confidence intervals

running at 32 mm SL (Fig. 2). Ripe males ranged from 32 to 62 mm. A seasonal difference was found in mean gonad stage in female *L. hectoris* ($F=50.7$; $DF=7,137$; $P<0.01$) which, from pair-wise t -tests, was significantly higher in April, June and August ($P<0.01$) than in other months (Fig. 3). Ripe females were present mainly in August 1984, when mean water temperature was below 13°C (Fig. 1). Maturing females were found in April and June 1984 and one maturing female was found in June 1985 (Fig. 2). A seasonal difference was also found in male gonad activity ($F=16.1$; $DF=4,56$; $P<0.01$). Ripe and ripe-running males of *L. hectoris* were found between June and October, with ripe-running males contributing 71% of males

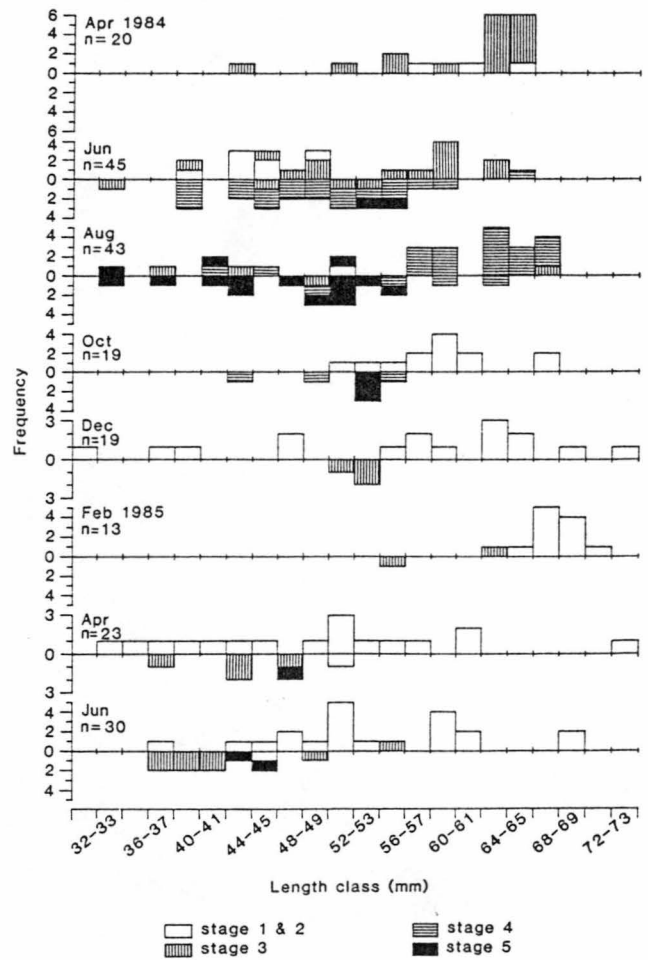


Fig. 2. *Lampanyctodes hectoris*. Gonad stages determined by histology from fish sampled between April 1984 and June 1985. In this, and similar figures, top histograms for each month represent females, bottom histograms males

sampled in August (Fig. 2). Gonad stages were significantly higher ($P < 0.01$) (Fig. 3) at this time than in the following autumn.

As the regression slopes of log (GSI) vs log (SL) for each two monthly period were parallel and significantly different from zero ($F = 21.7$; $DF = 1, 136$; $P < 0.01$), seasonal differences in GSI values were tested using ANCOVA (see "Materials and methods – Data analysis"). A seasonal difference in GSI of females was found ($F = 120.2$; $DF = 7, 136$; $P < 0.01$), with significantly higher values in June and August 1984 and June 1985 ($P < 0.01$) (Fig. 3). A seasonal difference was found in male GSI values ($F = 8.0$; $DF = 4, 56$; $P < 0.01$), with significantly higher values in June and August ($P < 0.05$). There was no relationship between size and GSI in males.

Gonadosomatic index was correlated with gonad stage, as determined by histological examination, in both females ($r_s = 0.68$, $DF = 141$; $P < 0.01$) and males ($r_s = 0.36$, $DF = 55$; $P < 0.005$) of *Lampanyctodes hectoris*.

Fecundity The fecundity of *Lampanyctodes hectoris* was determined from fish taken in June ($N = 16$) and August 1984 ($N = 19$). Egg counts ranged from 1 309 to 2 798 ($\bar{x} = 1\,956 \pm 101.9$ SE) in fish from 51 to 70 mm ($\bar{x} = 62.55$ mm ± 1.18 SE). A significant correlation existed ($r = 0.57$, $DF = 18$; $P < 0.01$) between the number of eggs and standard length. The relationship between fecundity (Y) and length (X) was $\ln Y = 1.585 \ln X + 1.0027$. There was no correlation between egg size and standard length. Egg size per fish ranged from 0.317 to 0.499 mm.

In all fish examined, a single mode of mature or maturing eggs was present in a matrix of smaller (< 0.3 mm) translucent eggs. However, in one fish taken in June 1984, a bimodal distribution of egg size was found: the smaller mode was at the lower egg-size limit (0.3 mm; Fig. 4), while the larger mode was comparable in size to the planktonic eggs of *Lampanyctodes hectoris* (Robertson, 1977). This bimodal distribution points to multiple spawning.

Description of male gonad. The testes appear to be of the "unrestricted spermatogonial testis-type" (Grier, 1981: p. 348) typical of most teleosts: the spermatogonia are not confined to small peripheral cysts within the tubule, but are spread along its length. The spermatogonia are, however, more prominent in some localities. Nearer to the sperm duct, sperm are a major component of the ripe testis. Interstitial cells are present as a triangular mass of tissue between the tubules.

The spermatozoa are unusual in being aflagellate. No sperm tails or midpieces were visible at the light microscope level in any histological section in which spermatozoa were found. In these sections, the spermatozoa are crescent or sickle-shaped; some appear to be twisted, which may be an artefact of preparation.

After ion-etching, the spermatozoa are clearly visible under the scanning electron microscope (Fig. 5). They are approximately to 3 to 4 μm in length. The pointed distal tip appears blunted at this magnification, but the wide

base appears slightly rounded or flat. In *Lampanyctodes hectoris*, the sperm head stains uniformly blue with haematoxylin and little cytoplasm is apparent around the nucleus.

Sex ratio. As sexual dimorphism is not obvious in *Lampanyctodes hectoris*, only gonads checked by histology were used in determining sex ratio. The overall female to male ratio was 2.16:1 ($N = 212$). Sex ratios differed between months, and the number of females relative to males increased over summer (Table 2). Sex ratios differed significantly with size ($\chi^2 = 41.83$, $DF = 4$; $P < 0.001$), with the ratio of females to males increasing steadily from an initial 1:1 ratio in fish less than 40 mm (Table 3). No males greater than 70 mm SL were recorded.

Maurolicus muelleri

Seasonal changes in gonad development and gonadosomatic index. Ripe females of *Maurolicus muelleri* ranged in size from 38 mm to 53 mm SL, although no ripe females between 40 and 44 mm SL were found. Mature males were generally smaller, ranging in size from 34 to 46 mm SL. Reproductive activity began in August 1984 and continued until December 1985 (Fig. 6). Gonads of both sexes were immature in February and April 1985. Female gonad stage differed significantly between months ($F = 75.0$; $DF = 6, 88$; $P < 0.01$). The high August, October and December values were significantly different ($P < 0.01$) from other months (Fig. 7).

Male gonad stage also differed seasonally ($F = 26.8$; $DF = 2, 27$; $P < 0.01$), with the highest stage in October and December ($P < 0.01$).

The regression slopes of log (GSI) vs log (SL) in females were significantly different from zero ($F = 76.5$; $DF = 1, 87$; $P < 0.01$) so an ANCOVA, with length as the independent variable, was used to test for seasonal differences in GSI. A significant difference between months ($F = 43.2$; $DF = 6, 87$; $P < 0.01$) in female GSI was found. Gonadosomatic indices in August, October and December were significantly higher ($P < 0.01$) than in other months (Fig. 7). No difference was found in GSI between August and October, but these values were significantly higher ($P < 0.01$) than in December, which suggests that August–October was the time of peak spawning.

Because of the low numbers of males in some months, only samples from June, October and December were tested. There was significant difference in GSI between months ($F = 8.0$; $DF = 4, 58$; $P < 0.01$); October and December 1984 values were significantly higher ($P < 0.01$) than those of June 1984 (Fig. 7).

In *Maurolicus muelleri* the gonadosomatic index was correlated with gonad stage, determined by histological examination in females ($r_s = 0.75$, $DF = 87$; $P < 0.01$) and males ($r_s = 0.57$, $DF = 34$; $P < 0.01$).

Fecundity. The fecundity of *Maurolicus muelleri* was examined in maturing and ripe fish sampled in October and

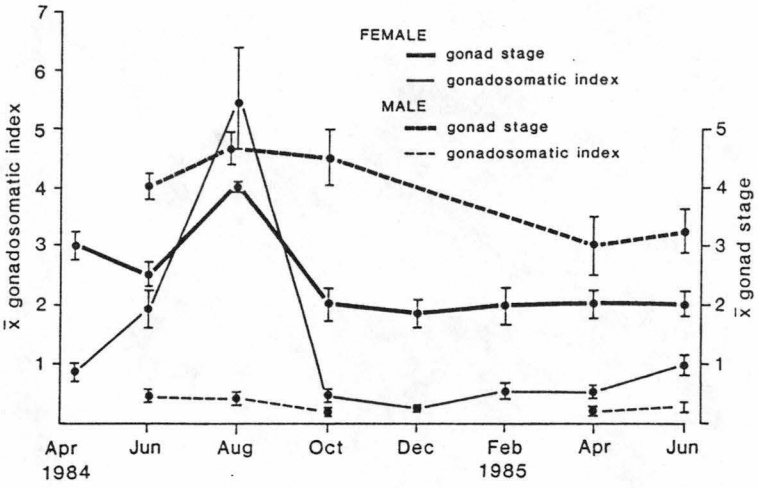


Fig. 3. *Lampanyctodes hectoris*. Mean gonadosomatic indices and mean gonad stages for females and males between April 1984 and June 1985. Bars define 95% confidence intervals

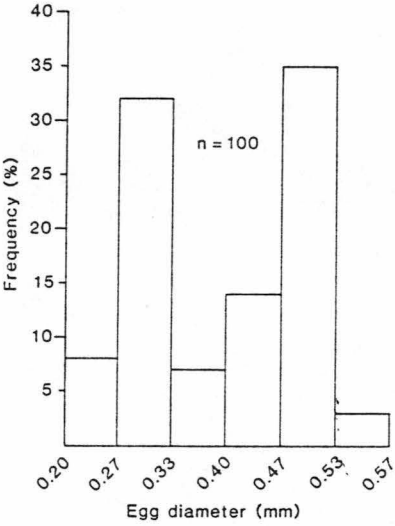


Fig. 4. *Lampanyctodes hectoris*. Size distribution of eggs from mature female (70 mm SL) taken in June 1984. N=number of eggs measured

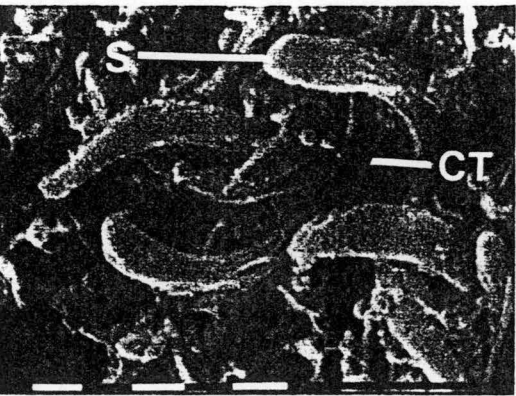


Fig. 5. *Lampanyctodes hectoris*. Scanning electron micrograph of mature spermatozoa (10 000x magnification; scale interval = 1 μm). CT: connective tissue; S: mature spermatozoon

Table 3. *Lampanyctodes hectoris*. Ratio of females to males in relation to size (standard length). N: number of fish in each size class

SL (mm)	♀	♂	N	♀:♂
≤40	13	13	26	1.0:1
41-50	32	29	61	1.1:1
51-60	48	23	71	2.0:1
61-70	48	1	49	48.0:1
≥71	3	0	3	— ^a

^a No males > 70 mm were recorded

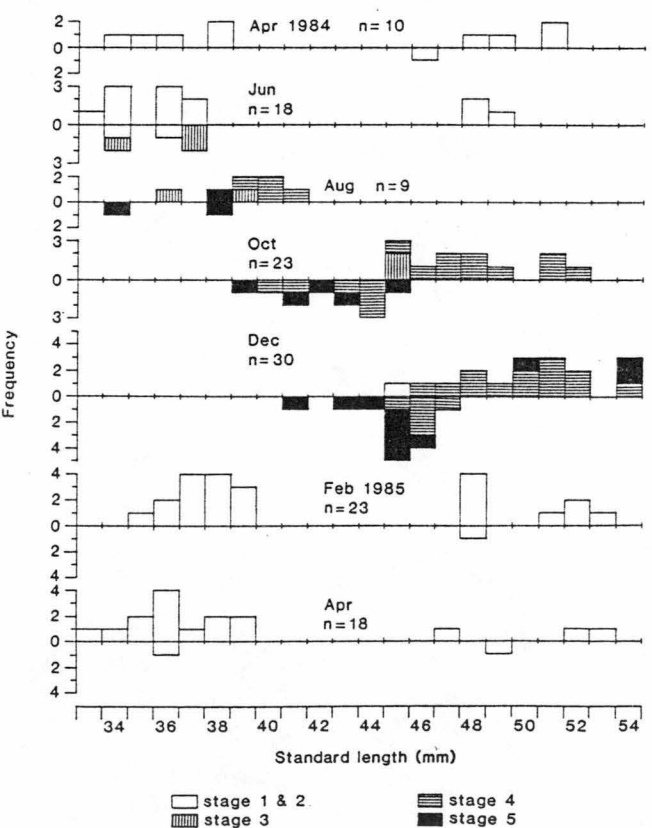


Fig. 6. *Maurolicus muelleri*. Gonad stages for females and males, determined by histology from fish sampled between April 1984 and April 1985

December 1984. Egg counts ranged from 104 to 942 ($\bar{x}=376\pm45.23$ SE) in fish ranging in size from 43 to 54 mm ($\bar{x}=49.09\pm0.64$ SE; $N=22$). Egg size ranged from 0.53 to 0.84 mm. There was no correlation between fish size and number or size of eggs over the length range examined.

Bimodal distributions in egg size occurred in all fish examined from a trawl made at 20.40 hrs on 14 December (Fig. 8a). The larger mode (approx 1.10 mm) corresponded with egg sizes reported from the plankton (Robertson, 1976). Fish examined from trawls immediately afterwards (00.08 hrs, 15 December) (Fig. 8b) and subsequently on 16

Table 4. *Maurolicus muelleri*. Ratio of females to males in relation to size (standard length). N : number of fish in each size class

SL (mm)	♀	♂	N	♀:♂
≤ 35	11	3	14	3.7:1
36–40	36	7	43	5.1:1
41–45	5	17	22	0.3:1
46–50	23	9	32	2.5:1
≥ 51	20	0	20	— ^a

^a No males > 50 mm were recorded

Table 5. *Diaphus danae*. Ratio of females to males in relation to size (standard length). N : number of fish in each size class

SL (mm)	♀	♂	N	♀:♂
≤ 50	13	0	13	— ^a
51– 60	2	0	2	— ^a
61– 70	7	5	12	1.4:1
71– 80	9	11	20	0.8:1
81– 90	9	18	27	0.5:1
91–100	9	8	17	1.1:1
101–110	17	0	17	— ^a
111	5	0	3	— ^a

^a Males absent

December, contained only eggs of the smaller mode (> 0.50 mm), indicating that spawning had occurred between 14 and 15 December. As the smaller mode was significantly larger than the size of maturing ova reported by Clarke (1982), a further spawning was considered likely.

Sex ratio. The overall ratio of females to males was 2.64:1 ($N=131$). Sex ratios differed between months (Table 2), but there was no consistent pattern. A significant difference in sex ratios between length classes occurred (χ^2 , 39.69, $DF=4$; $P<0.001$); females outnumbered males in each size class, except the 41 to 45 mm class, where males were more numerous (Table 4). No males greater than 50 mm were recorded.

Diaphus danae

Seasonal changes in gonad development and gonadosomatic index. No actively maturing or ripe females of *Diaphus danae* were found (Fig. 9). Macroscopic examination of many more ripe females showed that this was not a sampling artefact. Maturing males were found between October 1984 and June 1985. One ripe male was found in October, but no ripe females were found. Sperm were of the aflagellate type described for *Lampanyctodes hectoris*.

No significant seasonal differences in female GSI occurred, and values were low (below 1.00) throughout the study period. A linear correlation existed between gonadosomatic index (Y) and fish SL (X). ($\ln Y=0.0206 \ln X-3.085$; $r=0.83$, $DF=63$; $P<0.001$).

Sex ratio. The ratio of females to males in *Diaphus danae* for all months combined was 1.64:1 ($N=111$). No consistent seasonal pattern in sex ratios was found. Sex ratios differed significantly with size ($\chi^2=47.42$, $DF=4$; $P<0.001$) (Table 5): males were absent from the two largest and two smallest size classes.

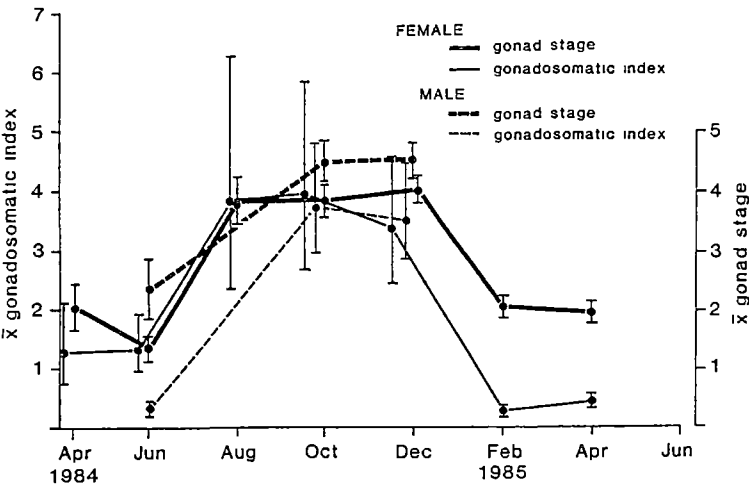


Fig. 7. *Maurolicus muelleri*. Mean gonadosomatic indices and mean gonad stages for females and males between April 1984 and April 1985. Bars define 95% confidence intervals

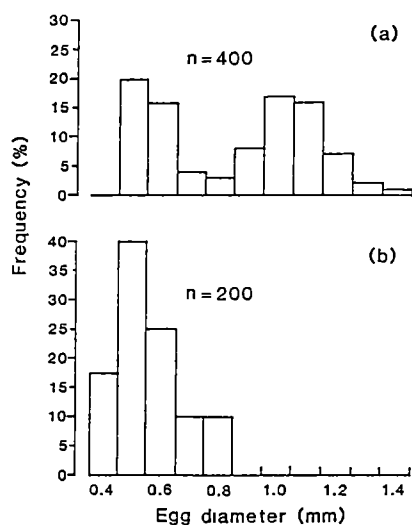


Fig. 8. *Maurolicus muelleri*. Size distribution of eggs from mature females taken on (a) 14 December 1984 and (b) 15–16 December 1984. N = number of eggs measured

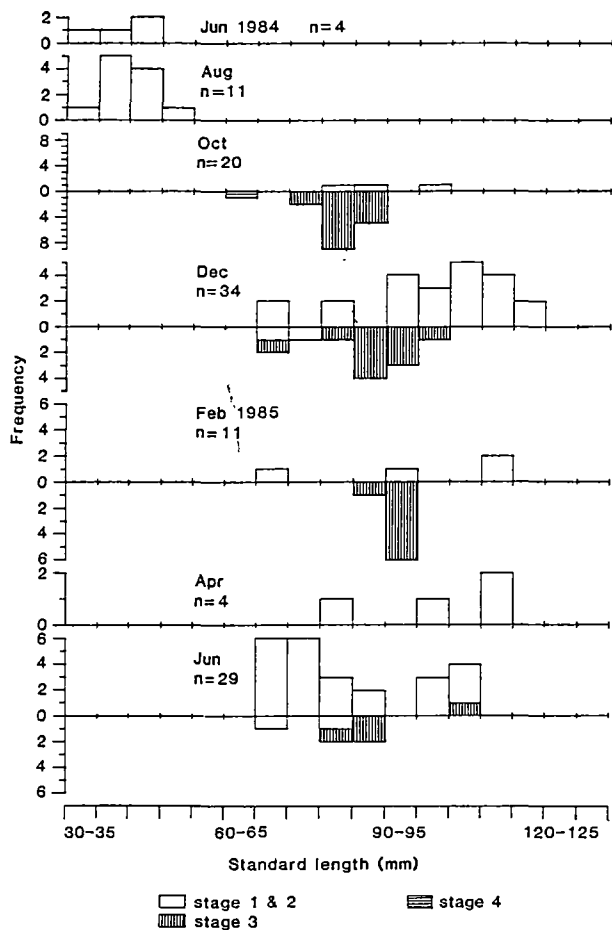


Fig. 9. *Diaphus danae*. Gonad stages for females and males, determined by histology from fish sampled between June 1984 and June 1985

Discussion

Spawning periods

Spawning in *Lampanyctodes hectoris* started in June (winter) and continued until October, with peak spawning in August. *Maurolicus muelleri* spawned mainly from August (late winter) to October, although ripe and spent females collected in December indicated that the spawning season of this species continues until early summer.

Myctophids in temperate and subtropical waters generally spawn from late winter to summer (Fast, 1960; Odate and Ogawa, 1961; Halliday, 1970; Smoker and Percy, 1970; Goodyear *et al.*, 1972; Clarke, 1973; Go *et al.*, 1977; Karnella and Gibbs, 1977). This is also true for the sternoptychid *Maurolicus muelleri* (Okiyama, 1971; Robertson, 1976; Gjosaeter, 1981a; Clarke, 1982). Clarke (1973) postulated that reproductive cycles in midwater fishes, particularly myctophids, were timed to coincide with the spring bloom (and the consequent increase in zooplankton abundance). In subarctic and subantarctic waters, however, spawning in some species of myctophids is confined to winter (Smoker and Percy, 1970; Robertson, 1977), as with *Lampanyctodes hectoris* in this study. According to Gjosaeter and Kawaguchi (1980: p. 22), winter spawning in high latitudes may be "an adaptation to low water temperature, since hatching takes much longer than in low latitudes." As juveniles of *L. hectoris* were present in the water column off Maria Island during late spring, when zooplankton abundance was increasing, early spawning may ensure that enough of the young of the year have reached maturity to take full advantage of the increased zooplankton production. *M. muelleri* spawned later, however, and juveniles were not present in the water column until February (Young, unpublished observations). This may be explained by the relatively larger egg size of *M. muelleri* (approximately twice that of *L. hectoris* eggs). Egg volume has been positively correlated with larval size at hatching in pelagic spawners (Blaxter and Hempel, 1963). Therefore, the initial development of *M. muelleri* may be synchronized to the occurrence of larger plankters occurring later in the spring plankton succession (thus reducing competition for the available food). This possibility is supported by Okiyama (1971), who found that early postlarvae of *M. muelleri* "can directly take the larger and much advanced organisms" (Okiyama, 1971: p. 22) of the plankton.

No spawning period was identified for *Diaphus danae*. Large individuals of *D. danae* (>70 mm) were not collected in June or August 1984, when reproductive maturity was most likely. However, as large *D. danae* were equally likely to be captured then as at other times of the year, it is possible that the population of *D. danae* off Maria Island was an expatriate one (Ekman, 1953). This is similar to observations reported for myctophid species in other waters (O'Day and Nafpaktitis, 1967; Zurbrigg and Scott, 1972; Gjosaeter, 1981b), where populations exist vegetatively outside their spawning area.

Fecundity

Although data are limited, fecundity in myctophids is approximately proportional to body length (Gjosaeter and Kawaguchi, 1980). Kawaguchi and Mauchline (1982) reported that larger myctophid species have higher fecundities (e.g. *Benthosema glaciale* 33 mm SL, < 300 eggs; *Lampanyctus macdonaldi* 123 mm SL, 7 072 eggs). In the present study, fecundity and length were positively correlated in *Lampanyctodes hectoris*, as reported by Gjosaeter and Kawaguchi (1980) for *B. glaciale*.

Different relationships between fecundity and length in *Maurolicus muelleri* have been reported. Clarke (1982) found that fecundity was proportional to length in individuals examined off south-eastern Australia; Okiyama (1971), Badcock and Merrett (1976), Gjosaeter and Kawaguchi (1980) and the present study found no relationship. However, Macgregor (1968) pointed out that the relationship between fecundity and length is unclear unless the largest fish in the sample is more than twice as long as the smallest fish. The ratio in the present study was only 1.3:1, whereas in Clarke's (1982) study it was 1.5:1, which may explain the different results. The fecundity of *M. muelleri* reported here compares very closely with that reported elsewhere (e.g. Okiyama, 1971), which suggests that the fecundity of this species shows little latitudinal variation.

Multiple spawning

The presence of different-sized modes of yolked oocytes suggests multiple spawning, usually over several months of the year (Le Clus, 1979). This assumes that all yolked cells are capable of developing to maturity, although total or partial resorption is possible (Macer, 1974). Smoker and Percy (1970) argued that the presence of a smaller mode of gametes in the myctophid *Stenobrachius leucopsarus* did not necessarily imply multiple spawning, as the immature gametes could either be expelled into the plankton or resorbed. Similarly, Tåning (1918) could not confirm multiple spawning in myctophids from the Mediterranean Sea.

Nevertheless, there is supporting evidence for multiple spawning in *Lampanyctodes hectoris*. In some marine fish (e.g. *Trachurus symmetricus*), the presence of an intermediate size mode of yolked oocytes indicates multiple spawning (Macgregor, 1976). In these fish, further evidence for more than one spawning can be found (e.g. an extended spawning season). In the present study, such a mode was present in one mature female of *L. hectoris*. Also, the individual examined came from the start of the reproductive season (June), which suggests that a further spawning was likely.

The evidence for multiple spawning in *Maurolicus muelleri* is stronger. Not only were bimodal distributions of egg-size present in many individuals, but also reproductive activity continued over an extended period

(Fig. 7), which is consistent with multiple spawning (Milton and Arthington, 1983; Williams and Clarke, 1983). Previous examinations of egg sizes of *M. muelleri* (Okiyama, 1971; Gjosaeter, 1981a; Clarke, 1982), and growth studies (Yuuki, 1984) also support this conclusion.

Sex ratios

Midwater fishes off Hawaii were found generally to exhibit a 1:1 ratio of females to males, with some exceptions, particularly among larger myctophid species where "females were either more abundant or larger than males" (Clarke, 1983: p. 203). In the present study all three species showed, overall, a positive bias in the ratio of females to males and a decline in the proportion of males with increasing size. Seasonal trends were apparent only in *Lampanyctodes hectoris*, perhaps due to small sample sizes. However, in some trawls, sexed subsamples, particularly of the myctophids, contained either all females or all males, which suggests that spatial segregation of sexes (Klingbeil, 1978) may occur. Other factors such as species size (Clarke, 1983), depth distribution (Badcock and Merrett, 1976) and differential avoidance of nets (Klingbeil, 1978) may have accounted for the bias towards females in this study. However, similarly biased catches of *L. hectoris* were reported off South Africa (Crawford, 1980). Possibly this bias is as an adaptation to "maximize egg-producing biomass" (Clarke, 1983: p. 203) in waters where food reserves are low. This may be the case in the present study, as maturing females (excluding *Diaphus danae*) are present before the onset of the spring bloom, when food may still be limited.

Sperm structure

The testes conform to the usual teleost pattern. However, the structure of the sperm is unusual. Although aflagellate sperm are found in several teleost families (Mattei, 1970), the sperm of *Lampanyctodes hectoris* and *Diaphus danae* resemble normal flagellate sperm, but without midpiece or tail. O'Day and Nafpaktitis (1967) reported that the sperm of the myctophid *Lobianchia dofleini*, which is very similar in shape to that of *Lampanyctodes hectoris*, does have a flagellum. However, they gave no evidence for this conclusion.

Other aflagellate sperm have simple cell-like bodies. The sperm of *Gymnarchus niloticus*, for example, are rounded cells with a central nucleus (Mattei *et al.*, 1967). The sperm of *Lampanyctodes hectoris* and *Diaphus danae* on the other hand go through the complex stages of sperm-head formation typical of most vertebrate species, but neither a midpiece nor tail is visible. The functional implication of an aflagellate sperm, which suggests limited mobility, is unclear. Perhaps, because these species occur in dense aggregations (May and Blaber, in preparation) and, for *L. hectoris* at least, males are reproductively active

for longer than females (Fig. 2), there is less need for a mobile sperm.

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CHAPTER 6

**Age and growth of the lanternfish, *Lampanyctodes hectoris*
(Myctophidae) from eastern Tasmania, Australia.**

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Age and growth of the lanternfish *Lampanyctodes hectoris* (Myctophidae) from eastern Tasmania, Australia

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Abstract

The age, growth and mortality of the lanternfish *Lampanyctodes hectoris* (Gunther) were investigated by examining the otoliths, length-frequency data, and seasonal abundance of fish collected from continental slope waters of eastern Tasmania between April 1984 and June 1985. Although *L. hectoris* can live to 3 yr old, it has a high annual mortality (79%) and few live past their first year. Growth, described here by a variation of the Von Bertalanffy model, takes place mainly in the first six months of life and only during late spring and summer. The hypothesis of daily deposition of primary growth increments in myctophids was supported by comparing the back-calculated birth dates of daily-aged individuals of *L. hectoris* with the spawning season of this species.

Introduction

Information on the age and growth of myctophid fishes is limited, particularly in the southern hemisphere, most studies having concentrated on northern hemisphere or tropical species (e.g. J. Gjosaeter and Kawaguchi 1980, H. Gjosaeter 1987). Moreover, in many species, age and growth have been estimated from reproductive cycles and length-frequency data (e.g. Clarke 1973, Karnella 1987). Estimates of mortality are also scarce (Gjosaeter and Kawaguchi 1980). Recent studies of tropical myctophids (J. Gjosaeter et al. 1984, H. Gjosaeter 1987) have shown the presence of primary growth increments corresponding to the daily increments found in the otoliths of coastal fishes (Campana and Neilson 1985). However, these increments have yet to be validated as daily.

Lampanyctodes hectoris is a wide-spread species in the southern hemisphere, abundant in continental slope waters of southern Africa (Ahlstrom et al. 1976, Crawford 1980), south-east Australia (Anonymous 1977) and New Zealand (Robertson 1977). This species was found to constitute more

than 90% of the biomass of fishes associated with the continental slope of eastern Tasmania (May and Blaber in preparation), and was the main prey of most fish species in these waters (Bulman and Blaber 1986, Blaber and Bulman 1987). However, the biomass of *L. hectoris* varies seasonally, with a ten-fold increase in summer (May and Blaber in preparation). Similar changes in biomass, together with seasonal variations in the length-frequency of this species, have also been reported off South Africa (Crawford 1980).

Based on previous studies of ageing, myctophids generally are fast-growing (Childress et al. 1980), have relatively short life spans and a high rate of mortality (Gjosaeter and Kawaguchi 1980). Whether these factors were responsible for the annual cycle in the biomass of *Lampanyctodes hectoris* off eastern Tasmania was examined using length-frequency data, otolithic ageing and seasonal abundances of fish sampled between April 1984 and June 1985. Primary growth increments were investigated as a means of more accurately describing growth in the early life-history of this lanternfish.

Materials and methods

Collection of material

Samples of *Lampanyctodes hectoris* (Gunther) were collected from the upper continental slope, 22 km east of Maria Island, Tasmania (42° 39'S; 148° 28'E) every two months from April 1984 to June 1985. Briefly, samples were collected using an Engel midwater trawl with a 10 mm cod-end liner, from discrete depths between the surface and 400 m, day and night. Full details are given in Young and Blaber (1986). Random samples of up to 500 fish per trawl were measured (standard length, SL, mm) and length-stratified sub-samples were either frozen or preserved in 70% alcohol. In the laboratory, fish were measured and the sagittae and lapilli removed and stored on glass slides in immersion oil.

Otolith examination

Whole sagittae were examined under the light microscope ($6\times$ magnification) in water on a black background, using incident light. The following observations were recorded:

- (i) number of hyaline and opaque zones, based on the terminology of Jensen (1965) (Fig. 1 a);
- (ii) length of the longest axis;
- (iii) width of the marginal increment along the longest axis. The marginal increment was defined as the distance from the outer edge of the last complete hyaline zone to the otolith margin.

Annuli were validated by comparing changes in the width of the marginal increment of sagittae of fish sampled between June 1984 and June 1985, using analysis of variance (ANOVA) (Warburton 1978, Sainsbury and Whitelaw 1984). This treatment has an advantage over earlier validation techniques (e.g. Saetersdal 1953), as it also gives an indication of growth rate.

Age in years was calculated from the number of hyaline and opaque zones observed. Dependent on validation, sagittae without a complete hyaline zone were defined as being in the 0+ yr class. Each additional opaque zone designated subsequent year classes. The age of each sagitta was determined independently by two readers; if the readings did not agree, the otolith was discarded.

Daily ages

To calculate daily age, the number of increments in the lapilli of 0+ fish were examined. Each lapillus was polished with carborundum powder and examined under a high-resolution compound microscope at 750 to $2\,000\times$ and an image-enhancing, closed-circuit television, following general procedures discussed by Campana and Neilson (1985). Only fish taken up to 6 mo after the 1984 spawning season were used; older fish could not be aged by light microscope because their increments were too closely spaced toward the lapillus margin, and thus below the level of microscope resolution (Campana and Neilson 1985). Daily ages were calculated as the number of increments present in the otolith. They were validated by comparing their back-calculated birth dates (date of collection less otolith age) with the spawning period for the species, as determined independently from the maximum gonadosomatic index, which Young et al. (1987) had shown to be correlated with the spawning time of this species. Each lapillus was read twice and was discarded if counts differed by more than 5%. The mean value of counts within the 5% limit were used in the analyses.

Data analysis

Length-frequency distributions were analysed using the computer program MIX (Macdonald and Green 1985),

which is based on an earlier program designed to fit normal distributions to polymodal data (Macdonald and Pitcher 1979). The resulting mixtures were interpreted from age-length data obtained from otoliths collected in each sampling period.

Fish were assigned an age in months relative to an arbitrary birthdate of 1 September, which is during the time when this species spawns (Young et al. 1987). Using this date a fish estimated as Age 1+, caught in December 1984, was considered to be 16 mo old. The ages of fish less than 6 mo old were determined from daily increments and converted to months. The combined data were fitted by a "switched growth" Von Bertalanffy curve (Pitcher and Macdonald 1973). This has the advantage over the simpler von Bertalanffy model in that it calculates "the proportion of time spent growing in each age class" (sw) and "the times of year at which the zero growth period begins and ends" (s) (Pitcher and Macdonald 1973, p. 600). This model is particularly useful if growth is seasonal.

The mean number of individuals per trawl in each sampling period was calculated and an age-length key was used to estimate the age structure of the catch. From this data a catch curve was constructed (Gulland 1969). Total instantaneous mortality (Z) was estimated from the slope of the descending limb of the catch curve, using log-linear regression (Ricker 1975). To minimise differences in year-class strength, mortality was estimated for all sampling periods combined (Gjosaeter 1973). Estimates of mortality may be biased by net selectivity, but the Engel 152 (used in this study), has been shown to sample a wider size range of fish than do other smaller-meshed nets (Young and Blaber 1986).

Results

Otolith description

The sagittal otoliths of *Lampanyctodes hectoris* are similar to those of other myctophid species (e.g. Gjosaeter 1981), possessing a wide, opaque central area surrounded by alternating hyaline and opaque zones (viewed by reflected light on a dark background) (Fig. 1 a). The sagittae are slightly elongate, the anterior margin is pointed, with a crenate margin along the ventral surface. Sagittae range in size from 1.38 to 2.26 mm (along the longest axis) in fish of standard lengths of 32 to 62 mm. The lapilli are ovoid to square in shape; the proximal surface is convex, the distal surface flattened. They range in size from 0.34 to 0.84 mm in fish of the same length as above.

Otolith analysis

Sagittae were examined for 290 individuals of *Lampanyctodes hectoris*, collected between June 1984 and June 1985 (Table 1). Nine otoliths were unclear and these were discarded.

Table 1. *Lampanyctodes hectoris*. Number of fish from which otoliths were examined from each year class for each sampling period between June 1984 and June 1985 (n = number examined). Numbers in parentheses: no. of fish from which lapilli were examined. Sagittae without complete hyaline zone defined as 0+ yr class; each additional opaque zone designated subsequent year classes

Age	1984				1985			n
	June	Aug.	Oct.	Dec.	Feb.	Apr.	June	
0+	7	7	8 (8)	40 (18)	37 (15)	45	43	187
1+	5	8	41	10	6	3	5	78
2+	0	0	8	0	6	0	2	16
Total	12	15	57	50	49	48	50	281

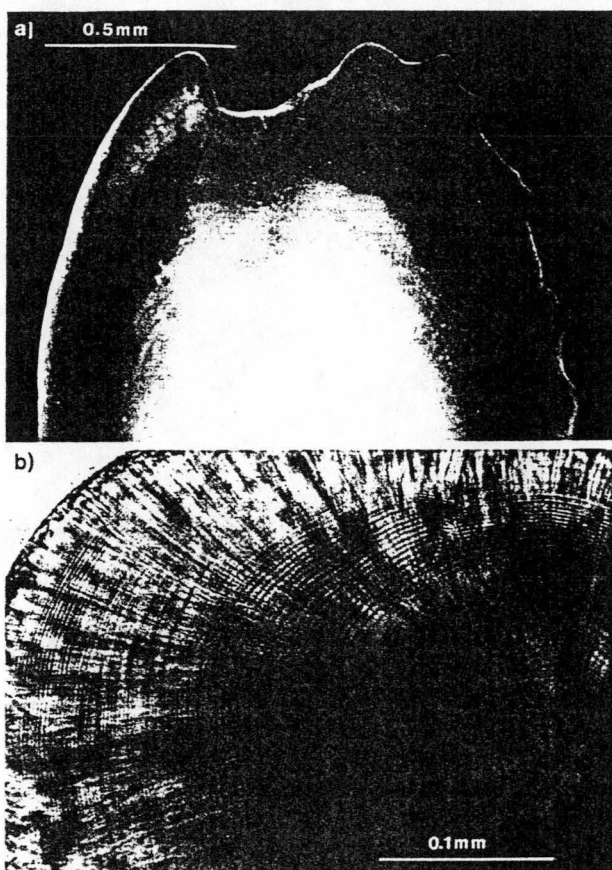


Fig. 1. *Lampanyctodes hectoris*. (a) Sagitta of an Age 1+ fish; (b) lapillus of a 100 d-old fish. (Both light micrographs)

There was a significant difference in the width of the marginal increment between seasons for otoliths with one (ANOVA, $F=24.63$; $DF=6.64$; $P<0.001$) and two (ANOVA, $F=19.34$; $DF=2.13$; $P<0.001$) hyaline rings (Fig. 2). The delineation of the hyaline zone and the subsequent formation of the new opaque zone was shown by a decline in the mean marginal increment in fishes sampled in October 1984. Rapid growth of the opaque zone, represented by increases in the marginal increments of fish with one and two hyaline rings, occurred over spring and summer. Based on these observations, each hyaline-opaque sequence

represented one year's growth. Two age groups were identified using this technique (Fig. 3). Fish in which the first hyaline zone had not yet been delineated were considered to be Age 0+ fish. There was a linear relationship between fish SL in mm (x) and sagittal length in mm (y) ($y=1.36x+41.4$, $r^2=0.89$, $DF=279$, $P<0.001$). Hence, the increase in sagittal size from October to December in 0+ fish indicated a rapid period of growth (Fig. 2). A spring-summer growth period was also evident in the otolith margins of Age 1+ and 2+ fish.

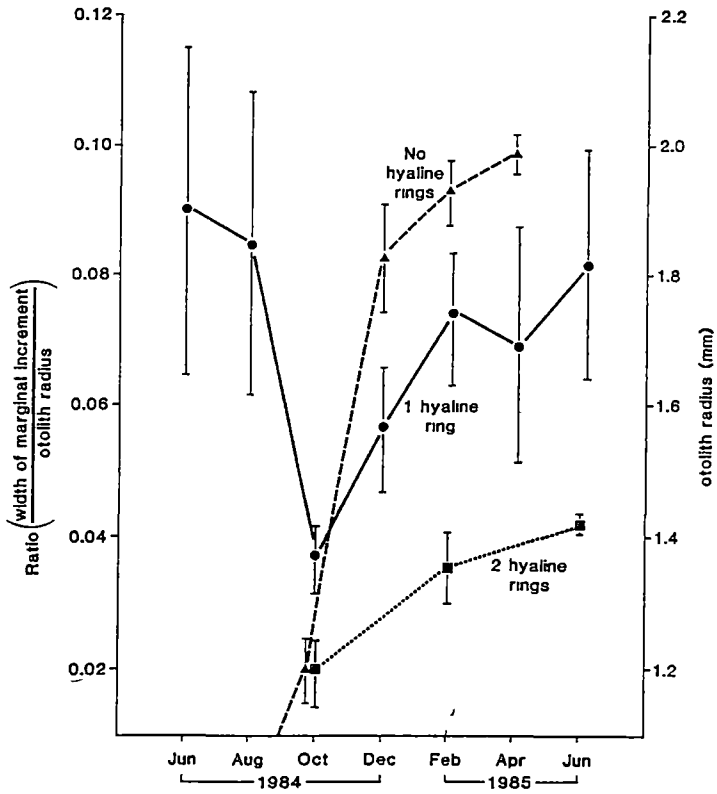
Length-frequency analysis

Three modal classes were identified in April 1984 (Fig. 4, Table 2) and, from the age-at-length data, corresponded to 0+, 1+ and 2+ year classes (Fig. 3). These modes were still present in June and August, although the proportion of 0+ fish declined markedly. In October, a new mode of recruits appeared, becoming the main component of the distribution by December, at which time two modes were present: recruiting juveniles and a mode consisting of 1+ and 2+ fish (not separable by the Macdonald-Pitcher analysis). Between February and June 1985, the proportion of 1+ and 2+ fish to 0+ fish declined. Differences in the size structure of populations of *Lampanyctodes hectoris* in April 1984 and April 1985 – the 2+ mode was barely present in 1985 – indicated that recruitment and mortality vary interannually.

Growth rates derived from modal analysis were very similar to the growth rates derived from otolith analysis (Table 2, Fig. 5). Otolith analysis, however, was more useful in separating the 1+ and 2+ modes during 1985, because these age classes were similar in length.

Daily ages

Lapilli from 47 fish taken between October 1984 and February 1985 were examined for microstructural increments (Table 1). There was disagreement on the increment counts of six fish and these were discarded (see "Materials and methods – Daily ages"). Each lapillus had an inner, middle and outer group of increments (Fig. 1b). In the inner group, increment counts ranged between 16 and 24 ($\bar{x}=22.2$,



◀ Fig. 2. *Lampanyctodes hectoris*. Seasonal changes in marginal increments (expressed as ratio of width of marginal increment to otolith radius) of sagittae of Age 1+ and 2+ fish (left-hand axis). Right-hand axis refers to increase in otolith radius of fish with no hyaline ring present (± 2 SE)

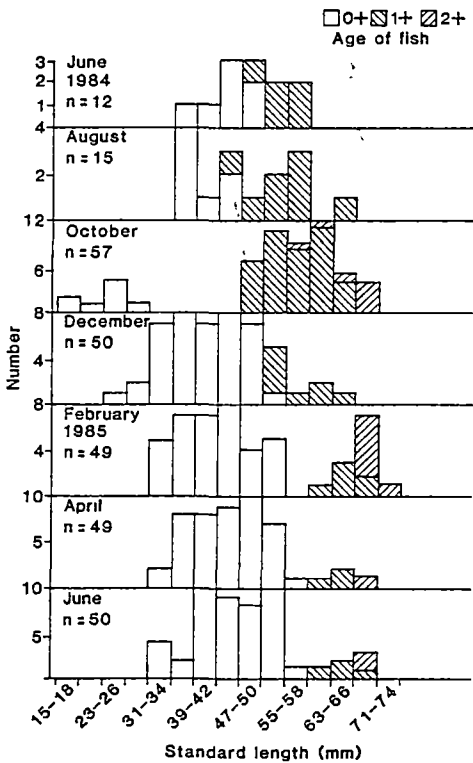


Fig. 3. *Lampanyctodes hectoris*. Length-frequency distributions of Age 0+, 1+ and 2+ fish, derived from otolithic ageing

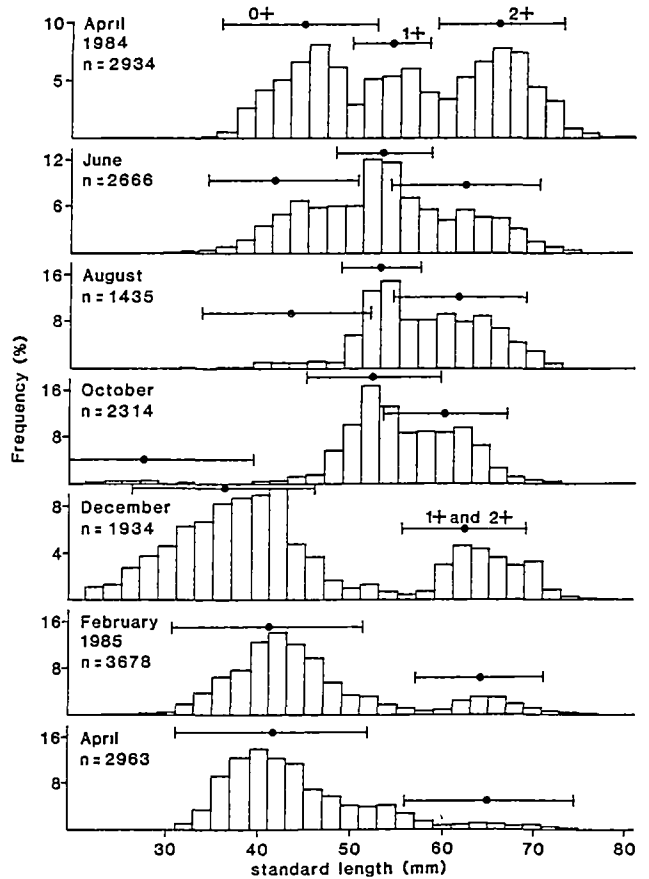


Fig. 4. *Lampanyctodes hectoris*. Length-frequency distributions of fish sampled between April 1984 and April 1985 off eastern Tasmania (± 2 SE)

Table 2. *Lampanyctodes hectoris*. Parameters (Par.) of Macdonald-Pitcher length-frequency analysis between April 1984 and June 1985 [\bar{x} : mean size of mode (standard length in mm); S : standard deviation of mode; P : relative abundance of mode as proportion of total sample] χ^2 : chi-square value; DF: degrees of freedom

Month	Par.	Year class (standard deviation)			χ^2 (DF)
		0+	1+	2+	
1984					
Apr.	\bar{x}	44.38 (0.36)	54.83 (0.36)	65.32 (0.19)	6.7 (3)
	S	4.39 (0.16)	2.20 (0.40)	3.78 (0.14)	
	P	0.45 (0.02)	0.16 (0.02)	0.40 (0.12)	
June	\bar{x}	43.38 (0.63)	52.48 (0.26)	62.35 (0.66)	4.3 (3)
	S	4.39 (0.31)	2.73 (0.43)	4.34 (0.35)	
	P	0.35 (0.04)	0.35 (0.06)	0.30 (0.32)	
Aug.	\bar{x}	42.45 (0.63)	52.14 (0.31)	61.38 (0.69)	4.7 (3)
	S	4.51 (0.91)	2.03 (0.22)	3.47 (0.27)	
	P	0.06 (0.01)	0.38 (0.05)	0.56 (0.05)	
Oct.	\bar{x}	28.98 (1.21)	51.89 (0.36)	61.12 (0.57)	82.7 (5)
	S	6.68 (1.25)	3.77 (0.22)	3.47 (0.27)	
	P	0.03 (0.01)	0.65 (0.05)	0.33 (0.05)	
Dec.	\bar{x}	36.02 (0.19)	62.74 ^a	(0.25)	6.9 (2)
	S	5.05 (0.07)	3.28	(0.57)	
	P	0.75 (0.01)	0.25	(0.01)	
1985					
Feb.	\bar{x}	41.32 (0.09)	64.31	(0.67)	67.2 (7)
	S	5.05 (0.07)	3.28	(0.57)	
	P	0.95 (0.02)	0.05	(0.01)	
Apr.	\bar{x}	42.57 (0.16)	64.36	(1.01)	67.2 (7)
	S	5.04 (0.11)	4.50	(0.67)	
	P	0.95 (0.02)	0.05	(0.01)	
June	\bar{x}	46.27 (0.11)	65.84	(0.32)	157.7 (6)
	S	5.24 (0.09)	2.58	(0.26)	
	P	0.95 (0.04)	0.05	(0.01)	

^a The 1+ and 2+ modes were not separable by modal analysis after October 1984, so are reported as one

SD=1.3). Increments in the middle group were difficult to distinguish and were probably the result of metamorphosis from the larval to juvenile form. Increment counts in this series ranged from 5 to 9 (\bar{x} =6.5, SD=1.3). Increments in the outer region made up the remainder of the count. Up to 135 increments were distinguished in this group. The relationship between standard length (y) and total increment number (x) was described by the exponential equation:

$$y = 26.27 \ln(x) - 86.27 \text{ (DF=38, } r^2=0.77, P<0.001 \text{)} \text{ (Fig. 6).}$$

To test whether increments were laid down daily, we assumed each increment represented one day. The birthdate was then calculated back from the time of sampling. The back-calculated spawning dates coincided with the spawning period of *Lampanyctodes hectoris* in 1984 (Fig. 7), indicating that growth increments in these fish were deposited daily. The slight offset between time of gonad maturation and spawning time may be explained by a lag in hatching time, which is common in high-latitude fish (Gjosæter and Kawaguchi 1980).

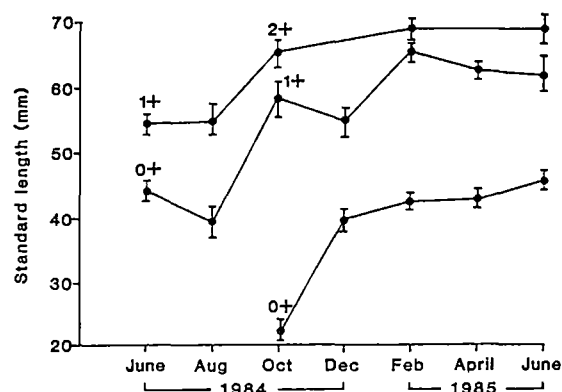


Fig. 5. *Lampanyctodes hectoris*. Growth rates of age classes derived from otolith analysis (± 2 SE)

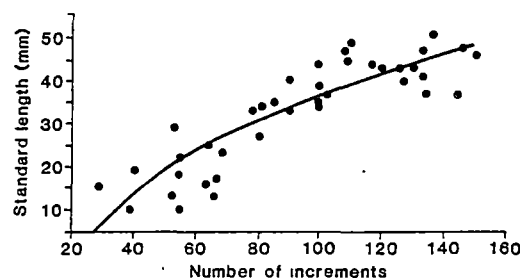


Fig. 6. *Lampanyctodes hectoris*. Relationship between standard length and number of increments in juvenile fish

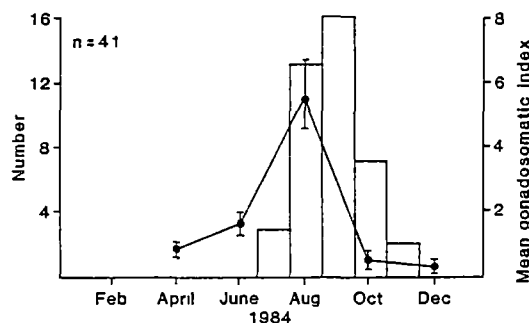


Fig. 7. *Lampanyctodes hectoris*. Back-calculated birthdates of Age 0+ fish estimated from daily increments (histogram). Right-hand axis refers to mean gonadosomatic indices ($\pm 95\%$ confidence limits) of mature females for same period (data from Young et al. 1987)

Growth curve

Most growth occurred within six months of spawning, with little growth thereafter (Fig. 8). Sagittal (annual) data could not, therefore, accurately describe the initial growth phase of *Lampanyctodes hectoris*. Consequently, daily ages were used in the growth curve for fish less than six months old. This was done after a significant correlation was found between ages as determined by the two ageing techniques (Spearman rank-correlation coefficient, 0.82, DF=39, $P<0.001$). Sagittal data was used for fish older than 6 mo.

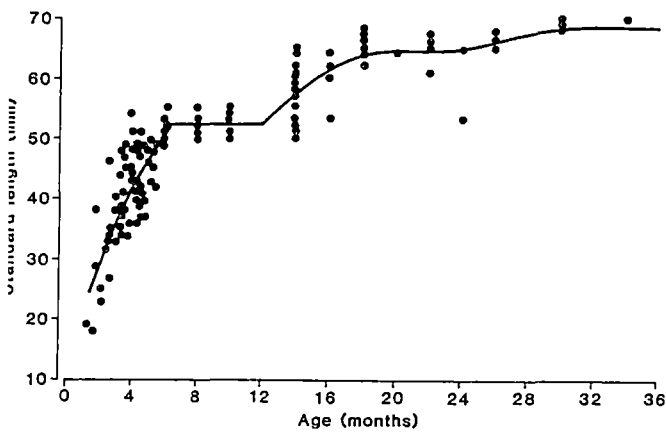


Fig. 8. *Lampanyctodes hectoris*. Growth curve from daily increments and annual data

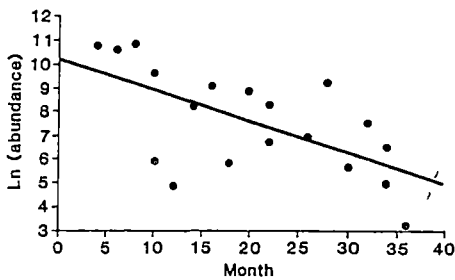


Fig. 9. *Lampanyctodes hectoris*. Relative abundance of each age class versus age in months

A switched-growth von Bertalanffy curve (Pitcher and MacDonald 1973) was fitted to the data with parameters: $L_{\infty} = 70.09$ (± 1.959 SE), $K = 0.0062$ (± 0.0007 SE), $t_0 = 0.921$ (± 0.39 SE), $s = 96.41$ (± 10.29 SE), $sw = -0.08$ (± 0.14 SE), where L_{∞} is the asymptotic maximum size, K the rate of proportional growth, and t_0 is the time in months (see "Materials and methods - Data analysis" for s and sw). There was a significantly better fit to the data using the "switched-growth" model as opposed to the typical von Bertalanffy growth model ($F = 18.7$, $DF = 2, 153$, $P < 0.01$). The former accounted for 85% of the variance, whereas the latter accounted for 81%. The model determined that growth stops 6.4 mo from the birthdate, and that there are 6.38 mo of growth per year. These values are supported by the length-frequency data.

Mortality

The natural logarithms of abundance of each age class was plotted against age in months for each sampling period (Fig. 9). The 0+ fish from October 1984 were not fully recruited (i.e., not on the descending limb of the catch curve) and therefore were not considered in the regression analysis. The descending limb of the catch curve was described by the equation

$$y = -0.132x + 10.209 \quad (r^2 = 0.38, DF = 18, P < 0.001).$$

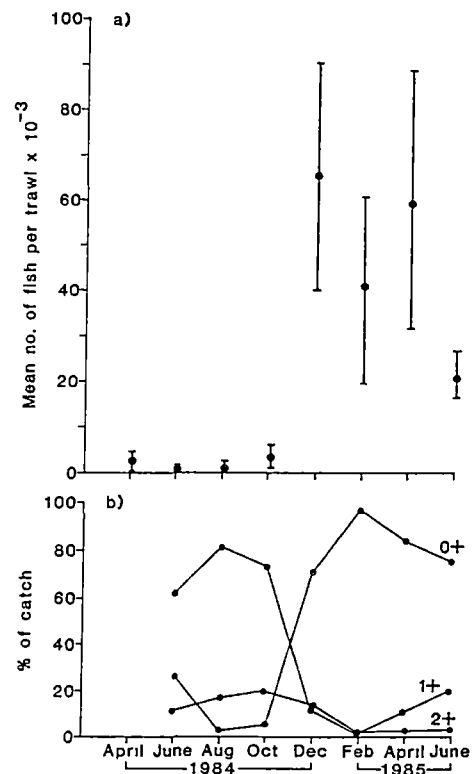


Fig. 10. *Lampanyctodes hectoris*. (a) mean abundance per sampling period (± 2 SE); (b) changes in proportion of each age class between seasons

The instantaneous rate of total annual mortality was estimated to be 1.58 (95% confidence intervals 0.55 to 2.25), which corresponded to an annual mortality of 79% (95% confidence intervals 45 to 92%) of the sampled population.

Examination of the mean catch by season indicated that mortality occurred mainly in summer and autumn (Fig. 10a). The proportion of adults (particularly 1+ fish) to 0+ fish declined markedly at the beginning of summer, followed by a decline in 0+ fish in autumn (Fig. 10b). If there were no interannual variability in the numbers of fish between years, then the autumn decline in numbers should reach that of the previous year (compare mean numbers for April 1984 with April 1985 in Fig. 10a). As this was not the case, interannual variability in recruitment strength is also indicated.

Discussion

The present study found that *Lampanyctodes hectoris* lives up to 3 yr, and attains a maximum size of 73 mm SL. In South Africa, a caudal length of 120 mm has been recorded; no maximum age was reported (Crawford 1980). However, other cold-water myctophids have been reported to live up to 5 yr (Odate 1966, Halliday 1970, Smoker and Pearcy 1970).

The population of *Lampanyctodes hectoris* consisted of three year-classes during most of 1984, and was dominated by adults. However, in December, newly recruited juveniles dominated the length-frequency distributions. Similar changes in the proportion of recruits to adults were found in *L. hectoris* off South Africa (Cruickshank 1983), although recruits entered the population later (January) in these waters.

Growth

Growth was confined to spring and summer, the time when warm-tropical East Australia Current waters interact with the subtropical convergence producing peaks in temperature, nutrients and primary productivity (Harris et al. 1987). Euphausiids, the main prey of *Lampanyctodes hectoris*, are most abundant at this time (see Young and Blaber 1986). Rapid growth in summer has also been reported for other temperate myctophid species (Gjosaeter 1973, Go et al. 1977, Kawaguchi and Mauchline 1982). There are exceptions: Kawaguchi and Mauchline (1982) found that myctophid species living in deeper waters did not show seasonal changes in growth, possibly because they would be less affected by seasonal hydrographic changes (e.g. temperature, food availability) than would shallower-living species such as *L. hectoris*.

Growth occurred mainly during the first six months of life, the growth curve approaching an asymptote quickly, which is typical of mesopelagic fishes (Childress et al. 1980). Juveniles grew by 15 to 20 mm in 2 to 3 mo, very similar to the growth rate of juvenile *Lampanyctodes hectoris* off South Africa (Cruickshank 1983). Growth slowed after the first year (at approximately 50 mm SL), which is when *L. hectoris* off Tasmania reach maturity (Young et al. 1987). Presumably the energy used for growth is diverted to gonadal development (Iles 1974).

Based on annual data, growth coefficients (K) for temperate myctophid species range from 0.11 to 1.05 and asymptotic length (L_{∞}) from 49 to 119 mm (Gjosaeter and Kawaguchi 1980). In South African waters, values for K and L_{∞} in *Lampanyctodes hectoris* were 0.31 and 99 mm, respectively (Anonymous 1972), both of which are higher than the values reported in this study ($K=0.006$, $L_{\infty}=70$ mm). This indicates that *L. hectoris* grow more rapidly, but to a smaller maximum size, off eastern Tasmania than off South Africa.

Daily ages

Rapid growth within the first year made it difficult to determine the growth of *Lampanyctodes hectoris* from sagittal data alone. Daily increments in fish otoliths, previously validated in studies of shallow-water fish (Panella 1974, Brothers et al. 1976), have been used to age myctophid fishes (J. Gjosaeter 1981, J. Gjosaeter et al. 1984, H. Gjosaeter 1987). For example, Gjosaeter (1987) fitted power curves (correlation coefficients >0.90) to length-at-age data using

daily ages in species of *Benthosema*. However, these studies, although providing strong circumstantial evidence that the increments observed were daily, were not able to validate their results. Back-calculation to a spawning peak was not possible, as the species in the above studies have extended spawning periods. The spawning season of *L. hectoris*, however, is well defined off eastern Tasmania, and as the back-calculated birthdates and spawning season of *L. hectoris* were concurrent, we were able to support the hypothesis that primary growth increments in myctophids are laid daily.

The middle group of increments in the lapilli of some specimens was difficult to read. Gjosaeter (1987), who found the same problem, suggested that, as this zone was not present in otoliths of larval myctophids, but was always present in metamorphosed fish, it was probably due to metamorphosis. Our observations support this conclusion.

Mortality

The rate of mortality of two myctophids, *Benthosema glaciale* and *Notoscopelus kroeyeri*, has been estimated in Norwegian waters as 0.74 and 0.8, respectively (Gjosaeter 1973, 1981). In *B. glaciale*, this is an annual mortality of 52%. The same species in the northwestern Atlantic has been reported to have an annual mortality of 83% (Halliday 1970), which indicates that mortalities may be highly variable within the same species of myctophid, although these differences could also reflect different sampling techniques. We found a 79% rate in the eastern Tasmanian population of *Lampanyctodes hectoris*; whether this is similar to other populations of *L. hectoris* is unknown, but the fact that the South African population is dominated by recruiting juveniles after summer suggests that mortality in adults is high in these waters also.

Conclusions

From the present study, we conclude that the seasonal cycle in the biomass of *Lampanyctodes hectoris* reflects: (1) recruitment and rapid growth of juveniles during spring, in response to increased availability of food (see Young and Blaber 1986); (2) high annual mortality after summer, possibly due to death after spawning (Clarke 1973, Karnella and Gibbs 1977), although predation (Blaber and Bulman 1987) and migration (Zurbrigg and Scott 1972) may also be important.

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CHAPTER 7

**Feeding ecology of three species of midwater fishes associated with
the continental slope of eastern Tasmania, Australia.**

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Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia

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Abstract

The feeding ecology of *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae* was examined from samples collected from continental slope waters of eastern Tasmania between April 1984 and April 1985. A total of 2 232 stomachs was analysed. *M. muelleri*, *L. hectoris* and *D. danae* fed primarily on euphausiids and secondarily on copepods, although larger *D. danae* (> 60 mm standard length) fed on other lanternfish (chiefly *L. hectoris*). The diets of *M. muelleri* and *L. hectoris* overlapped substantially. Diet overlaps between *D. danae* and the former species was low, however, due to the large biomass of fish present in *D. danae*. The prey taxa consumed changed with time of year and predator size. Stomach fullness (feeding intensity) varied seasonally in all three species, but only *M. muelleri* showed significant diel differences in fullness. The synchronization of the size structure of the predator populations and their feeding intensity, with seasonal variations in preferred prey, is proposed as a mechanism whereby each species maximizes its share of the available food resources.

Introduction

Mesopelagic fishes, dominated by the lanternfish *Lampanyctodes hectoris*, form dense aggregations over the upper continental slope off South Africa, New Zealand and southeastern Australia (Anonymous, 1977; Robertson, 1977; Crawford, 1980). Despite the fact that they are the major component of the pelagic fish biomass in these waters and are the main prey of many continental slope fishes (Clarke, 1982; Bulman and Blaber, in press), little is known of their basic biology.

Oceanic midwater fish are generally considered to be opportunistic feeders, migrating to surface waters at night to feed, mainly on crustacean zooplankton (Hopkins and

Baird, 1977; Clarke, 1978; Kinzer and Schulz, 1985). However, in regions of high productivity (usually close to land masses or in upwelling areas), less distinct feeding cycles have been reported (Kinzer, 1977, 1982). Diets are modified both by seasonal variations in zooplankton (Hopkins and Baird, 1977; Gjosaeter, 1981a, b) and individual predator size (Paxton, 1967; Tyler and Percy, 1975; Hopkins and Baird, 1977; Scotto di Carlo *et al.*, 1982). Gjosaeter (1981a) found that the diet of *Maurolicus muelleri* differed with season and size of individual, but found no evidence for diel feeding.

As part of a larger study of the community ecology and trophic structure of the continental slope fish-community of eastern Tasmania (Blaber, 1984), samples of the three dominant midwater-fish species – *Maurolicus muelleri* (family Sternoptychidae), *Lampanyctodes hectoris* and *Diaphus danae* (both family Myctophidae) – were collected for dietary analysis. This paper examines their feeding ecology in relation to seasonal and diel cycles and to the size of individuals.

Materials and methods

Maurolicus muelleri, *Lampanyctodes hectoris* and *Diaphus danae* were collected from 88 trawls over the upper continental slope (420 to 550 m depth) approximately twelve nautical miles east of Maria Island, Tasmania (42°39'S; 148°28'E) on seven cruises of F.R.V. "Soela" between April 1984 and April 1985. An "Engel 152" pelagic trawl was used after initial comparisons with two other trawls, the rectangular midwater trawl (RMT 8) and the International Young Gadoid Pelagic Trawl (YGPOT) had shown that the Engel net sampled a wider range of size classes of the target species (Fig. 1). Trawl depth was monitored with a Simrad FB Trawl eye mounted on the trawl headrope. During the first three cruises (April, June and August 1984) trawls were aimed at sound-scattering marks over the diel period and lasted approximately 40 min at depth. The next four

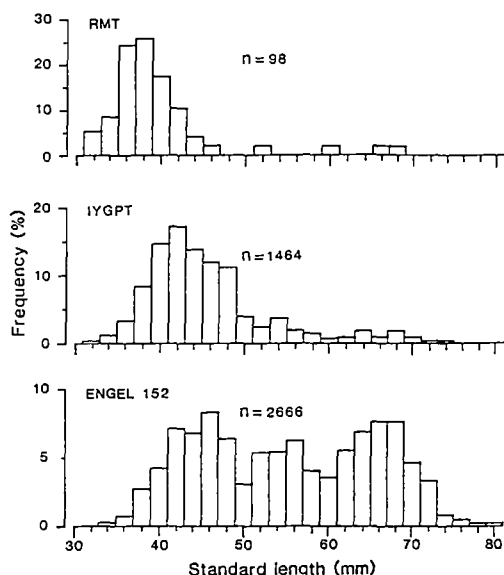


Fig. 1. *Lampanyctodes hectoris*. Length-frequency distributions from RMT-8, IYGPT, and "Engel 152" midwater trawls taken during April 1984. n: number of individuals

cruises (October and December 1984, and February and April 1985) employed a stratified random sampling strategy in order to determine abundance (J. May *et al.*, in preparation). This consisted of at least three replicate, 40 min tows within each of the depth strata of 10 to 60 m, 60 to 160 m, 160 to 260 m and 260 to 360 m made during daylight and repeated at night. No samples were taken at dusk or dawn because the depth distributions of the target species change at these times (Backus *et al.*, 1969). As net type, trawl duration, depths and area fished were the same for each trawling method, we assumed that the samples obtained throughout the year were directly comparable.

A sample of up to 20 fish of each species was taken from each trawl and immediately fixed in buffered seawater-formalin. Fish for stomach analysis were chosen from trawls made at 4 h intervals from midnight, and from the widest range of depth intervals. To minimize contamination from net-feeding (Clarke, 1978), fish with fresh prey in the mouth were discarded.

Fish for dissection were weighed (± 0.01 g) and measured (standard length, SL, ± 0.5 mm) and their stomachs removed. The wet weight of the stomach contents (± 0.01 mg) divided by the wet weight of the whole fish, gave a quantitative measure of stomach fullness expressed in g kg^{-1} of fish wet weight. The contents were then identified to the lowest possible taxon using the keys of Nyan Taw (1975) and Tafe (1979) for copepods, Kirkwood (1982) for euphausiids and Bowman and Gruner (1973) for amphipods. The total length (TL) of whole prey was measured with an ocular micrometer and converted to millimeters (± 0.1). The number (where possible) and wet weight of each prey taxon was recorded. The prey were then dried to constant weight at 60°C and the dry weight recorded for each taxon.

Diet was determined from the percentage dry weight (biomass) and percentage frequency of each prey taxon and was calculated only from fish containing prey. Dietary overlaps were measured from the biomass data using the percentage similarity index of Shorygin (Ivlev, 1961). This index ranges from 0 (no overlap) to 100% (complete overlap). Biomass data were used as this was the closest measure of caloric content available (Wallace, 1981).

Regression analysis was used to test for seasonal changes in the dry weight proportions of the major prey taxa. This analysis was used to construct analysis-of-variance tables, because the number of individuals and number of trawls taken varied within and between seasons. A parameter was fitted for each month and the hypothesis that all parameters were equal was tested with the *F* test. This test should not be greatly affected by non-normality (Clarke, 1978), as it tests for differences between means, which are asymptotically normal. Stomach fullness (feeding intensity) was also compared using regression analysis, with respect to month, time of day and depth. For each of these effects, the corresponding parameters were tested for equality with the *F* test. Time of day was divided into four 6 h intervals starting at midnight and depths into four 100 m intervals from the sea surface.

The relationship between fish length and prey type was examined using a contingency table with one nominal classification (main prey taxon by weight in a stomach) and one ordinal (predator length). The data were analysed with a loglinear model for an ordinal-nominal classification (Agresti, 1983). The initial hypothesis tested was that all size classes have the same proportions of major prey items (the "homogeneity" hypothesis). If this hypothesis was rejected, we tested the hypothesis that the proportions of each prey type changed linearly with predator size (the "column-effects" hypothesis).

Results

Overall diet and dietary overlap

A total of 719 stomachs of *Maurolicus muelleri* (78% contained prey), 975 stomachs of *Lampanyctodes hectoris* (81% contained prey) and 538 stomachs of *Diaphus danae* (91% contained prey) was analysed. The size range of individuals examined is given in Table 1. Euphausiids and calanoid copepods, respectively, were the main dietary components in *M. muelleri* and *L. hectoris* (Table 2), consequently dietary overlap between these species was high (Shorygin's index = 70.5). The major difference between *M. muelleri* and *L. hectoris* was that the latter consumed a relatively higher dry weight proportion of euphausiids and a wider range of prey taxa. The diet of *D. danae* consisted mainly of *L. hectoris*, copepods and euphausiids. Calanoid copepods were eaten in large numbers by *D. danae*, but accounted for less than 1% of the total prey biomass. Even though *D. danae* fed on many of the prey types of either *M. muelleri* or *L. hectoris*, or both, dietary overlap between *D. danae* and the former species was low (15.9 and 17.4, respective-

Table 1. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Size range of individuals examined for stomach contents. SL: standard length in mm; (n): number of fish examined

Month	<i>M. muelleri</i>		<i>L. hectoris</i>		<i>D. danae</i>	
	SL	(n)	SL	(n)	SL	(n)
1984						
April	29–52	(113)	31–73	(257)	29–116	(88)
June	29–51	(107)	35–65	(104)	34–76	(103)
August	31–42	(60)	37–73	(138)	34–71	(123)
October	32–55	(120)	27–69	(143)	55–119	(35)
December	32–54	(78)	27–72	(120)	66–122	(95)
1985						
February	28–54	(121)	34–71	(71)	64–121	(32)
April	29–53	(120)	34–73	(142)	66–122	(62)

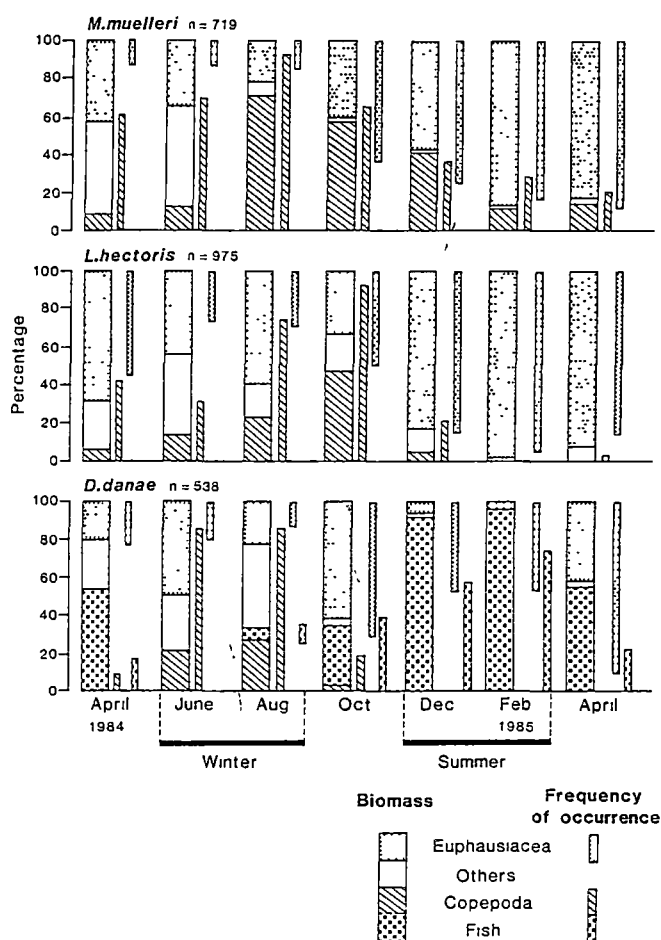


Fig. 2. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Seasonal changes in percentage (dry weight) biomass and frequency of occurrence of major prey taxa in stomachs. n: number of fish examined

ly). This was due to the predominantly piscivorous diet of *D. danae* in summer and autumn (Fig. 2). Other prey items that occurred less frequently, but which were important in the diet of all three species in certain months, were ostracods, hyperiid amphipods, crab larvae (only in *D. danae*), pelagic gastropods, salps and fish scales.

Seasonal changes in diet

Maurolicus muelleri

Copepods were the main prey consumed during winter and spring, whereas euphausiids dominated in summer and early autumn (Fig. 2). Significant seasonal differences were found in the prey biomass of calanoid and cyclopoid copepods, euphausiids and crustacean remains (Table 3). The calanoids *Candacia bipinnata* and *Pleuromamma abdominalis* were the main prey during June and August. The main calanoid species identified in October and December were *Neocalanus tonus* and *Euchirella rostrata*, respectively; the former was still occurring in stomachs in April 1985. The cyclopoids *Oncaea media* and *O. venusta* were eaten between April and October, and especially in August, but scarcely affected the overall prey biomass. *Euphausia similis* var. *armata* was the main euphausiid eaten during summer, although *Nematoscelis megalops* was also an important prey item. *Nyctiphanes australis*, an abundant shelf species (Nyan Taw, 1975), was rarely found in the fish examined. Fish scales and eggs were consumed intermittently.

Lampanyctodes hectoris

Euphausiids were the main prey of *Lampanyctodes hectoris* throughout the year except in August and October, when calanoid copepods were the main prey eaten (Fig. 2). Significant seasonal differences were found in the prey biomass of calanoids, hyperiid amphipods, euphausiids, crustacean remains and gastropods (Table 3). Between December 1984 and April 1985, *Euphausia similis* var. *armata* and, less frequently, *E. lucens*, *Nematoscelis megalops* and *Thysanopoda egregia* were the main euphausiids consumed, accounting for over 85% of both dry weight and frequency of occurrence values. During August, calanoid copepods, primarily *Lucicutia flavicornis* and *Pleuromamma* spp., contributed 21% dry weight; by October, they contributed 46% dry weight. *Calanoides caranatus*, *Metridia lucens*, and *Neocalanus tonus* occurred less frequently. The dry weight contribution by cyclopoids (*Oncaea media* and *O. venusta*) was very little (<1%) between April and October, although frequency of occurrence values were 20 to 35%. No cyclopoids were consumed after October.

Other prey were important during certain months. Salps were present during August and October, while gastropods were found in October and December. Hyperiid amphipods, mainly *Parathemisto gracillipes*, were consumed during August when they were common in the plankton (Young, unpublished data). Small amounts of fish (occasionally *Maurolicus muelleri*), fish scales and eggs were consumed between June and December.

Diaphus danae

Midwater fishes, mostly *Lampanyctodes hectoris* and occasionally *Maurolicus muelleri*, were the main prey con-

Table 2. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Composition of diets of fish from continental slope waters off eastern Tasmania % Biomass: % of total dry weight of prey; % F: % frequency of occurrence; n: number of stomachs examined; percentage totals for each main prey taxa are given in parentheses; -: prey absent

Prey	<i>M. muelleri</i> 28–55 mm SL 0.12–0.76 g DW ^a [0.30 ± 0.02 g DW] ^b (n = 719)		<i>L. hectoris</i> 27–73 mm SL 0.10–1.28 g DW ^a [0.65 ± 0.08 g DW] ^b (n = 975)		<i>D. danae</i> 29–122 mm SL 0.15–9.00 g DW ^a [2.07 ± 0.33 g DW] ^b (n = 538)	
	% Biomass	% F	% Biomass	% F	% Biomass	% F
Chaetognatha	(–)	(–)	(–)	(–)	(< 0.1)	(0.2)
Siphonophora	(–)	(–)	(0.6)	(0.1)	(–)	(–)
Crustacea	(98.7)	(99.0)	(93.3)	(98.2)	(17.2)	(81.4)
Ostracoda	(< 0.1)	(0.7)	(< 0.1)	(1.0)	(< 0.1)	(3.7)
Copepoda	(37.1)	(44.0)	(10.9)	(42.9)	(0.2)	(39.8)
Calanoida	36.5	42.5	10.7	38.0	< 0.1	38.6
<i>Acartia clausi</i>	–	–	–	–	< 0.1	0.2
<i>Calanoides caranatus</i>	0.1	2.5	< 0.1	0.5	–	–
<i>Calanus australis</i>	0.2	2.3	< 0.1	0.9	–	–
<i>Calanus finmarchicus</i>	–	–	< 0.1	0.1	–	–
<i>Candacia bipinnata</i>	0.9	5.0	0.5	3.7	< 0.1	4.7
<i>Candacia pectinata</i>	–	–	< 0.1	0.3	–	–
<i>Euchaeta marina</i>	–	–	0.2	0.8	–	–
<i>Euchirella rostrata</i>	2.2	2.9	< 0.1	0.4	–	–
<i>Euchirella</i> spp.	1.3	2.5	–	–	–	–
<i>Heterorhabdus papilliger</i>	–	–	< 0.1	0.1	–	–
<i>Lucicutia flavicornis</i>	–	–	5.7	7.1	< 0.1	0.2
<i>Metridia lucens</i>	< 0.1	0.2	0.1	1.9	–	–
<i>Neocalanus tonsus</i>	10.0	9.1	0.2	1.8	< 0.1	0.2
<i>Pleuromamma abdominalis</i>	3.4	9.8	0.3	5.2	< 0.1	5.3
<i>Pleuromamma gracilis</i>	< 0.1	0.2	0.7	11.2	< 0.1	6.3
<i>Pleuromamma remains</i>	1.7	3.2	0.8	8.3	0.1	23.5
Unidentified calanoids	16.5	30.3	2.0	25.8	< 0.1	11.4
Cyclopoida	0.7	20.3	0.2	15.5	< 0.1	4.7
<i>Corycaeus</i> spp	–	–	–	–	< 0.1	0.2
<i>Oithona</i> spp.	–	–	< 0.1	0.3	–	–
<i>Oncaea conferta</i>	–	–	< 0.1	0.3	–	–
<i>Oncaea media</i>	0.1	7.5	< 0.1	3.4	< 0.1	0.8
<i>Oncaea venusta</i>	0.6	19.4	0.1	13.4	< 0.1	3.5
<i>Oncaea</i> spp.	< 0.1	0.4	< 0.1	1.3	< 0.1	0.6
Leptostraca	(< 0.1)	(0.2)	(–)	(–)	(–)	(–)
Mysidacea	(–)	(–)	(0.1)	(0.3)	(–)	(–)
Amphipoda	(0.2)	(1.2)	(0.4)	(1.5)	(< 0.1)	(3.1)
Hyperiididae	–	–	0.2	0.6	< 0.1	1.2
<i>Parathemisto gracillipes</i>	–	–	0.2	1.3	< 0.1	0.4
Pronoidae	–	–	–	–	< 0.1	0.2
Amphipod remains	–	–	–	–	< 0.1	1.2
Euphausiacea	(54.8)	(51.1)	(78.5)	(59.1)	(14.9)	(36.5)
<i>Euphausia longirostris</i>	–	–	–	–	< 0.1	0.2
<i>Euphausia lucens</i>	–	–	3.1	3.8	1.3	2.2
<i>Euphausia similis</i> var. <i>armata</i>	18.9	12.3	34.7	21.6	9.0	26.3
<i>Euphausia</i> spp.	0.8	2.9	6.6	13.9	–	–
<i>Nematoscelis megalops</i>	1.4	1.1	0.5	1.6	0.7	0.6
<i>Nematoscelis microps</i>	–	–	< 0.1	0.1	–	–
<i>Nematoscelis</i> spp.	–	–	0.1	0.1	–	–
<i>Nyctiphanes australis</i>	0.1	0.2	< 0.1	0.1	–	–
<i>Thysanopoda egregia</i>	–	–	0.6	0.5	–	–
Unidentified euphausiids	30.9	32.9	33.1	19.1	3.8	8.0
Caridea (juveniles)	(–)	(–)	(< 0.1)	(0.1)	(0.1)	(0.6)
Brachyura (larvae)	(–)	(–)	(–)	(–)	(1.1)	(2.5)
Unidentified crustacean remains	(6.5)	(23.8)	(3.3)	(11.2)	(0.8)	(20.4)
Gastropoda	(< 0.1)	(0.2)	(1.5)	(5.8)	(< 0.1)	(0.8)
Bivalvia	(< 0.1)	(0.5)	(–)	(–)	(< 0.1)	(0.2)
Thaliacea (Salpidae)	(< 0.1)	(0.2)	(0.4)	(1.8)	(0.1)	(5.9)

Table 2 (continued)

Prey	<i>M. muelleri</i> 28–55 mm SL 0.12–0.76 g DW ^a [0.30 ± 0.02 g DW] ^b (n = 719)		<i>L. hectoris</i> 27–73 mm SL 0.10–1.28 g DW ^a [0.65 ± 0.08 g DW] ^b (n = 975)		<i>D. danae</i> 29–122 mm SL 0.15–9.00 g DW ^a [2.07 ± 0.33 g DW] ^b (n = 538)	
	% Biomass	% F	% Biomass	% F	% Biomass	% F
Pisces	(< 0.1)	(0.7)	(1.4)	(3.0)	(82.9)	(22.5)
<i>Lampanyctodes hectoris</i>	—	—	—	—	72.5	14.5
<i>Maurolicus muelleri</i>	—	—	—	—	10.0	0.8
Unidentified fish	< 0.1	0.5	—	—	< 0.1	1.4
Fish eggs	< 0.1	0.4	—	—	< 0.1	4.1
Fish scales	< 0.1	0.4	0.2	2.7	0.2	4.1
Unidentified remains	(1.3)	(6.2)	(3.3)	(23.5)	(—)	(—)
Dry weight range of stomach contents (mg)	0.1–22.1		0.5–25.0		10.2–555.2	
Mean dry weight of stomach contents (mg) ± SE (mg)	2.3 ± 0.24		1.8 ± 0.17		23.1 ± 3.66	

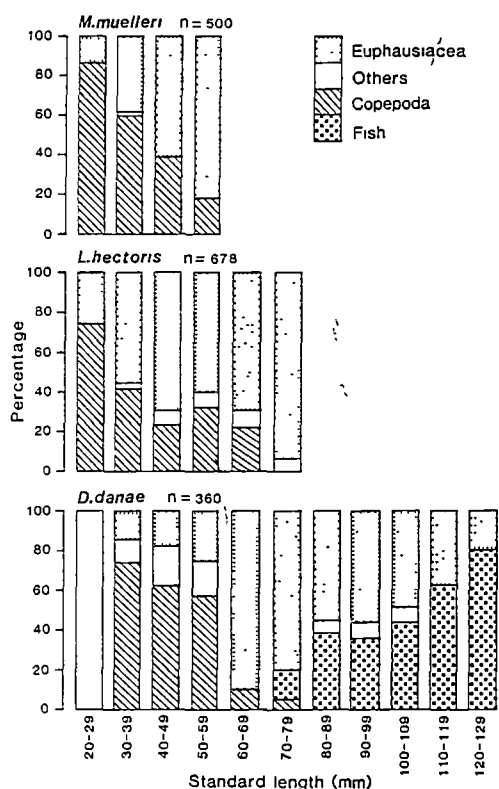
^a Dry weight range ^b Mean dry weight (± SD)

Fig. 3. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Frequency of occurrence of major prey taxa across size classes. n: number of fish examined

sumed by *Diaphus danae* in summer and autumn, whereas copepods and euphausiids were consumed at other times of the year (Fig. 2). There were significant seasonal differences in the prey biomass of calanoids, amphipods, euphausiids, salps and fish (Table 3). Calanoids, typically *Candacia bipinnata*, *Pleuromamma abdominalis* and *P. gra-*

cilis, were eaten between June and August, as were the cyclopoids *Oncaea media* and *O. venusta*. Euphausiids were consumed between April and December. In summer, *Euphausia lucens* and *E. similis* var. *armata* were the main euphausiids identified. Ostracods, hyperiid amphipods (families Hyperiididae and Pronoidae), salps, fish scales and eggs were consumed in small quantities between April and August. Crab larvae were consumed only in December and the following April.

Relationships between fish length and prey type

The hypothesis that the proportions of major prey taxa were homogeneous across size classes in *Maurolicus muelleri* was rejected. The hypothesis that the proportions of each prey taxon change linearly with predator size was retained (Table 4). The proportion of euphausiids in the stomach contents increased with increasing predator size, whereas the proportion of copepods decreased (Fig. 3, Table 4). It is noteworthy that the frequency of occurrence of cyclopoid copepods (< 3 mm TL) was 92% (107 out of a total of 113) in *M. muelleri* less than 40 mm SL, whereas the frequency of occurrence of calanoid copepods (3 to 8 mm TL) in the same fish was only 67% (146 occurrences out of 240).

Homogeneity of the proportions of prey taxa across size classes was similarly rejected for *Lampanyctodes hectoris*, although these proportions did not change linearly with predator size (Table 4). Nevertheless, euphausiids became predominant in the diet of larger individuals (Fig. 3). In addition, small gastropods (shell diam = 1.5 to 3.0 mm) were recorded mainly from individuals of 40 to 60 mm SL, while hyperiid amphipods (5 to 7 mm TL) were found chiefly in individuals of 50 to 60 mm.

Table 3. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Seasonal changes in prey biomass (mg dry weight) in stomachs between April 1984 and April 1985. Significance values for acceptance (NS) or rejection ($P < 0.05$) of the hypothesis that prey proportions do not vary with season are listed beside each major prey taxon. —: prey absent

Prey	<i>M. muelleri</i>								<i>L. hectoris</i>							
	Apr	June	Aug	Oct.	Dec.	Feb	Apr	<i>P</i>	Apr.	June	Aug	Oct	Dec.	Feb.	Apr.	<i>P</i>
Calanoida	4.5	7.7	57.7	291.7	135.7	32.0	29.2	<0.001	14.1	5.2	31.7	175.9	9.4	—	1.0	<0.001
Cyclopoida	6.2	6.1	0.1	—	—	—	—	<0.005	2.6	0.2	1.3	1.5	—	—	—	NS
Amphipoda	—	—	—	—	—	—	—	—	—	—	8.0	<0.1	—	—	—	<0.001
Euphausiacea	53.6	38.5	17.4	209.0	184.2	232.3	157.4	<0.01	243.9	20.5	93.6	136.9	142.6	353.5	268.9	<0.001
Crustacean remains	53.3	57.9	4.9	—	—	—	—	<0.001	—	17.2	7.7	37.1	—	—	—	<0.001
Gastropoda	—	—	—	—	—	—	—	—	—	—	—	17.9	—	—	—	—
Others	7.7	0.3	1.0	4.7	<0.1	—	3.7	NS	89.1	0.8	7.8	9.0	—	—	0.4	<0.001
Total dry wt of stomach contents (mg)	125.3	110.6	81.2	506.4	319.9	264.3	190.2		349.8	45.1	154.8	384.3	166.5	356.1	285.3	
Total dry wt of fish examined (g)	22.51	16.32	9.04	37.90	23.12	23.76	20.29		138.63	50.98	68.55	80.17	36.33	43.99	35.72	
g kg ⁻¹ fish dry wt (±SE)	5.57 (1.56)	6.78 (1.61)	8.98 (2.29)	13.36 (2.09)	13.84 (1.71)	11.12 (2.85)	9.37 (2.42)		2.52 (0.44)	0.89 (0.24)	2.26 (0.50)	4.79 (0.75)	4.58 (1.29)	8.09 (1.59)	7.98 (1.37)	
No. of stomachs with food	96	87	46	100	55	85	95		214	81	108	140	90	62	96	

Prey	<i>D. danae</i>							
	Apr.	June	Aug.	Oct.	Dec.	Feb.	Apr.	<i>P</i>
Calanoida	2.5	28.6	21.4	0.8	—	—	—	<0.001
Cyclopoida	<0.1	0.6	1.6	—	—	—	—	NS
Amphipoda	—	0.3	5.7	<0.1	—	—	—	<0.05
Euphausiacea	173.5	77.1	21.1	28.3	329.5	190.0	1411.9	<0.001
Crustacean remains	—	185.7	15.5	2.4	<0.1	—	—	NS
Gastropoda	—	—	—	—	—	—	—	—
Others	17.8	22.2	16.9	1.2	100.8	—	82.0	<0.001
Total dry wt of stomach contents (mg)	835.6	148.7	86.0	44.3	4278.5	3836.6	3183.3	
Total dry wt of fish examined (g)	281.25	50.05	42.87	85.40	287.13	141.51	272.94	
g kg ⁻¹ fish dry wt (±SE)	2.97 (1.24)	2.97 (0.91)	2.01 (0.41)	0.52 (0.14)	14.90 (4.80)	27.11 (10.19)	11.66 (2.43)	
No. of stomachs with food	88	100	116	34	70	26	56	

Prey type also varied with the size of *Diaphus danae* (Table 4). Copepods were progressively replaced by euphausiids in fish up to 60 mm SL. In larger individuals there was a shift from euphausiids to fish as the dominant prey (Fig. 3, Table 4). The low linearity measure for euphausiids reflects their predominance as prey of middle-sized *D. danae*.

As the main prey taxa of both *Maurolicus muelleri* and *Lampanyctodes hectoris* were copepods and euphausiids, we compared the proportions of the prey of these two species. *L. hectoris*, the larger predator, consumed a significantly higher relative biomass (84%; $P < 0.001$) of the

larger prey type, euphausiids, than did *M. muelleri* (64%). Conversely, *M. muelleri* fed on a relatively higher biomass of copepods.

Diet in relation to depth

Similar proportions of the major taxa were found above and below 160 m in all three species (Table 5). The proportions varied slightly in *Maurolicus muelleri* as the large number of small individuals from shallow depths contained chiefly copepods.

Table 4. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Relationship between fish length and prey taxa in stomachs. Values are number of occurrences of a taxon as the main prey by dry weight in a stomach, by size class. C: copepods; E: euphausiids; F: fish; O: other taxa; (n): number of stomachs examined

	<i>M. muelleri</i>			<i>L. hectoris</i>					<i>D. danae</i>				
	C	E	(n)	C	E	F	O	(n)	C	E	F	O	(n)
Size class (mm SL)													
20– 29	6	1	(7)	3	1	0	0	(4)	0	0	0	0	(0)
30– 39	171	116	(287)	45	62	1	0	(108)	30	6	0	5	(41)
40– 49	58	94	(152)	43	123	8	8	(182)	58	18	3	16	(95)
50– 59	9	42	(51)	71	126	3	11	(211)	6	3	2	0	(11)
60– 69				34	107	8	6	(155)	0	33	21	0	(54)
70– 79				0	17	0	1	(18)	1	16	1	2	(20)
80– 89									0	29	21	5	(55)
90– 99									0	33	21	6	(60)
100–109									0	12	11	2	(25)
110–119									0	14	24	0	(38)
120–129									0	1	4	0	(5)
Total no. of occurrences	244	253	(497)	196	436	20	26	(678)	95	165	108	36	(404)
Likelihood – ratio test statistics (G^2), degrees of freedom (DF) and significance levels for homogeneity and column-effects hypotheses													
	G^2	DF	P	G^2	DF	P	G^2	DF	P	G^2	DF	P	
Homogeneity hypothesis	46.18	3	< 0.001	35.86	9	< 0.001	293.4	21	< 0.001				
Column effects hypothesis	0.33	2	> 0.5	24.29	6	< 0.001	28.41	18	> 0.05				
Linearity parameters (values further from zero imply increasing linearity and are analogous to slope coefficients)													
Copepods		– 0.94			–						– 1.08		
Euphausiids		0.94									0.35		
Fish											0.80		
Others											– 0.07		

Table 5. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Percentage occurrence of major prey items in stomachs above and below 160 m depth. C: copepods; E: euphausiids; F: fish; (n): number of fish examined

Depth (m)	<i>M. muelleri</i>			<i>L. hectoris</i>			<i>D. danae</i>		
	C	E	(n)	C	E	(n)	E	F	(n)
≥ 160	58	42	(87)	37	60	(214)	55	43	(83)
≤ 160	46	54	(431)	29	66	(444)	53	40	(121)

Stomach fullness

A significant relationship ($P < 0.05$) between time of year and stomach fullness was found in *Maurolicus muelleri*, with the highest values recorded between June and October (Table 6), when copepods were the main prey. Lowest values occurred in February and April, 1985. Significant diel and depth differences indicated that *M. muelleri* fed mainly in the evening (18.00–24.00 hrs) ($P < 0.05$) above 200 m depth ($P < 0.05$). Stomach fullness values were significantly higher in *M. muelleri* than in either *Lampanyctodes hectoris* or *Diaphus danae* ($P < 0.05$) (Fig. 4).

In *Lampanyctodes hectoris*, a significant relationship ($P < 0.005$) existed between time of year and stomach full-

ness. Highest stomach fullness values were found in December and February (Table 6), when euphausiids were eaten almost exclusively (Fig. 2). Lowest values occurred during winter (particularly June). No significant diel or depth differences were detected, although Fig. 4 shows that feeding was more intensive between 18.00 and 24.00 hrs than at other times.

A significant seasonal relationship ($P < 0.005$) with stomach fullness was found in *Diaphus danae*. Stomach fullness values were highest in February 1985 (Table 6), when fish were the main prey. Lowest values were found in spring, when euphausiids were consumed. No significant diel or depth differences were detected, although stomach fullness values were generally higher in the evening (Fig. 4).

Discussion

The major prey taxa of *Maurolicus muelleri* and *Lampanyctodes hectoris* were euphausiids and copepods, respectively, while *Diaphus danae* fed mainly on other lanternfish (chiefly *L. hectoris*), copepods and euphausiids. The relative importance of the types of prey eaten, however, was dependent on the time of year and on the size of the individual predator. The importance of copepods

Table 6. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Bimonthly mean stomach fullness values (g stomach contents wet wt kg⁻¹ fish wet wt) between April 1984 and April 1985. Results of regression analyses are shown at bottom of table. (n): number of fish examined. *t* = Student's *t* test

	<i>M. muelleri</i>			<i>L. hectoris</i>			<i>D. danae</i>		
	<i>x</i>	± SE	(n)	<i>x</i>	± SE	(n)	<i>x</i>	± SE	(n)
1984									
April	16.6	4.9	(113)	9.5	1.5	(257)	11.7	2.7	(88)
June	22.3	5.0	(107)	3.0	2.3	(104)	14.6	2.2	(103)
August	19.9	6.8	(60)	6.0	2.0	(138)	8.7	2.0	(123)
October	21.9	4.7	(120)	8.6	2.1	(143)	3.6	3.8	(35)
December	15.2	5.6	(78)	15.7	2.0	(120)	12.6	2.3	(95)
1985									
February	12.5	4.7	(121)	13.2	2.8	(71)	24.1	4.0	(32)
April	9.2	4.7	(120)	8.8	2.0	(142)	14.0	2.8	(62)
	<i>(t</i> = 2.37; DF = 40; <i>P</i> < 0.05)			<i>(t</i> = 3.25; DF = 52; <i>P</i> < 0.005)			<i>(t</i> = 2.98; DF = 32; <i>P</i> < 0.005)		

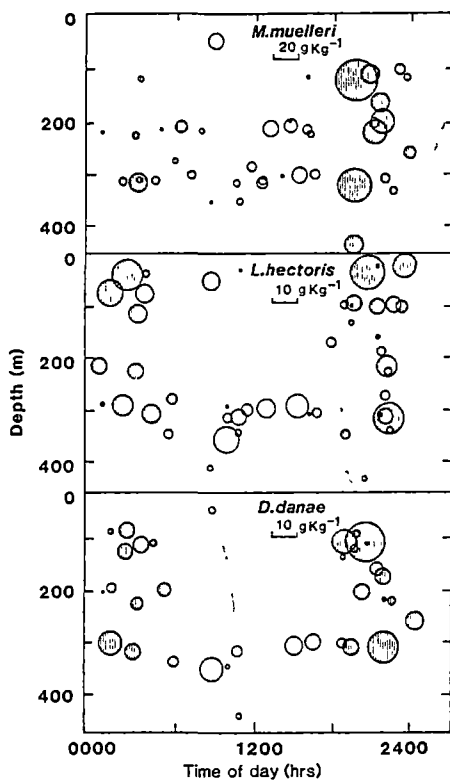


Fig. 4. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Stomach fullness in relation to depth and time of day. Each circle represents mean stomach fullness value per trawl; scale refers to diameter of circle; shaded circles represent hours of darkness

(Hopkins and Baird, 1977; Clarke, 1980; Kinzer and Schulz, 1985) and euphausiids (Paxton, 1967; Samyshev and Schetinkin, 1971; Tyler and Percy, 1975) as prey of midwater fish is well documented. Generally, euphausiids are more prevalent in midwater fish found in productive upwelling regions or waters close to land (as in this study) and copepods are the main prey of oceanic species. However, the predation of one myctophid species on another to

the extent shown by *D. danae* on *L. hectoris* has not previously been reported.

Dietary overlap was high between *Maurolicus muelleri* and *Lampanyctodes hectoris*. The copepods *Candacia bipinnata*, *Neocalanus tonsus*, *Pleuromamma* spp., species of *Oncaea*, and the euphausiids *Euphausia similis* var. *armata*, and *Nematoscelis megalops* were common to each predator, implying little dietary specialization. This phenomenon has been reported for other high-latitude midwater fish (Tyler and Percy, 1975). However, the overlap between *Diaphus danae* and the former species was low, even though all three species had many prey species in common (Table 2). This can be explained by the seasonal importance of *L. hectoris* in the diet of *D. danae*.

Marked seasonal differences in diet were found. Copepods were the dominant prey item in *Maurolicus muelleri* during late winter and early spring, being gradually replaced by euphausiids with the approach of summer. A similar pattern was observed in *Lampanyctodes hectoris*, although euphausiids were more prevalent throughout the year and dominated the diet of this species between December and April. Copepods and euphausiids were restricted mainly to winter and early spring in *Diaphus danae*, after which time fish became increasingly important and were the main prey consumed in summer. Seasonal differences in diet have also been reported by Gjosaeter (1981a), who found that *M. muelleri* off Norway consumed mainly copepods in spring, and euphausiids in winter. Similarly, the myctophids *Benthosema glaciale* and *Notoscopelus elongatus* ate euphausiids in winter and copepods during summer (Gjoesaeter, 1973, 1981b).

A seasonal change in diet is typical of temperate fishes. Hopkins and Baird (1977) suggested that it was related to seasonal changes in prey distribution and abundance. This is supported by data from eastern Tasmania. Nyan Taw (1975) reported that copepods were most abundant during winter and spring, which is when they most frequently occurred as prey of all three species. *Neocalanus tonsus*, one

of the few abundant summer copepods reported by Nyan Taw, was a frequent prey item of *Maurolicus muelleri* in the present study between October and April. Euphausiids are most abundant during summer (Nyan Taw, 1975; CSIRO, unpublished data). *Lampanyctodes hectoris*, the major prey of *Diaphus danae* between December and April, was also most abundant over the summer months.

Our results indicate that size-selective predation (O'Brien, 1979) may determine not only the types of prey eaten by all three species but may also be related to the size of the individual predator. Smaller individuals of *Maurolicus muelleri* fed on copepods, while larger fish ate euphausiids. Copepods were progressively replaced by euphausiids in *Diaphus danae* less than 60 mm SL; above this size, fish became increasingly important. In *Lampanyctodes hectoris*, although euphausiids were the main prey in all but the smallest size class, their importance increased with size. Similar results have been reported from other mid-water feeding studies. Gjosaeter (1981a) found that *M. muelleri* smaller than 20 mm fed primarily on copepods, while larger fish fed equally on copepods and euphausiids. Samyshev and Schetinkin (1971) also found a correlation between predator size and diet in *M. muelleri* and in species of *Diaphus*. Small individuals of another myctophid species, *Hygophum benoiti*, feed almost exclusively on copepods, while larger individuals take primarily euphausiids (Scotto di Carlo *et al.*, 1982).

No correlation was found between prey type and depth. This contrasts with the findings of Percy *et al.* (1979), who reported little similarity in either the diets or rank order of common prey of individuals of the myctophid *Stenobrachius leucopsarus* separated by depth in deep water off Oregon (USA). The slope-species studied here are distributed between the surface and approximately 500 m depth (CSIRO, unpublished data) and hence have a much narrower range in which to feed. As all three species migrate vertically, they are likely to encounter most prey types present in the water column.

Significant diel feeding-periodicity was found only in *Maurolicus muelleri*, which fed mainly at night above 200 m. This contrasts with the findings of Gjosaeter (1981a), who found no evidence for diel feeding in *M. muelleri*. In oceanic waters near Hawaii, Clarke (1978) found that nine of ten species of myctophid examined fed "solely or principally at night in the upper layers". This is perhaps true of most vertically migrating oceanic mid-water-fish (Hopkins and Baird, 1977; Kinzer and Schulz, 1985). Nevertheless, in more productive areas such as upwelling zones (Kinzer, 1977, 1982) or water close to land (Paxton, 1967; Tyler and Percy, 1975; Gjosaeter, 1981a, b), myctophids tend to feed continuously. This view is supported by the present study, although our results suggest that feeding was more intensive in both *Lampanyctodes hectoris* and *Diaphus danae* during the night (Fig. 4).

Synchronization of growth with availability of prey

Present results indicate that time of year and predator size were the major determinants of the type and amount of

prey eaten. Feeding intensity (as indicated by stomach fullness) and the size structure of the population may be synchronized with seasonal variations in prey abundance in order to maximize each species' share of the available food resource.

During August, when the mode of *Maurolicus muelleri* was less than 40 mm SL, feeding intensity was highest, and copepods, abundant during winter, were the main prey consumed. In October, the population mode had increased to 45 mm SL and euphausiids were becoming more important as prey. By December, when euphausiid abundance peaks, euphausiids dominated the diet and the maximum length had been reached. In *Lampanyctodes hectoris* feeding intensity was highest and juvenile recruitment occurred in summer, when euphausiids were abundant. Small *Diaphus danae* occurred during winter when copepods were abundant, but by summer had reached their maximum length and shifted to fish as their main prey; stomach fullness values were highest at this time.

In a similar feeding study of the three most abundant myctophids off Oregon, Tyler and Percy (1975) suggested that competition for the available food resource was reduced by spatial separation in the water column. We suggest competition may also be reduced by the synchronization of the seasonal growth cycles of each species with the abundance of its prey.

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CHAPTER 8

Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania.

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Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania

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Abstract. Crustacean microzooplankton were the main prey of larval *Trachurus declivis* collected in the summers of 1988, 1989 and 1990 from coastal waters of eastern Tasmania. The diet was dominated by harpacticoids (*Microsetella rosea*), cyclopoids (mainly *Oithona* spp.), calanoids and the calyptopis stage of the euphausiid *Nyctiphanes australis*. Bivalve veligers were occasionally eaten. Diets of larvae were affected by interannual variations in plankton composition, particularly in 1989 when intrusions of low-nutrient subtropical water excluded large zooplankters (e.g. *N. australis*) from the study area. Larvae ≤ 6 mm selected for copepod nauplii; all larvae selected for *M. rosea*, cyclopoids, and the calyptopis stage of *N. australis*. Even though calanoids were a major prey taxon, there were proportionally fewer eaten than were present in the environment. In all, 78% of larvae taken during the daytime had food in their stomachs, as opposed to 38% of the larvae from night samples. Feeding was restricted to daylight hours, with peaks in the mid-morning and late afternoon. A gut evacuation rate of ~4 to 6 h was estimated. We calculated that the larvae ate between 9 and 13% of their body weight in food per day. The larvae of *T. declivis* in this study were not sufficiently abundant to have an impact on their prey.

Introduction

Previous studies of the diet of larval fishes from temperate waters showed that predation by the larvae did not affect the abundance of their prey (e.g. Peterson and Ausubel 1984, Jenkins 1987). In particular, Jenkins estimated that larval flounder would have little or no impact on prey populations in an enclosed bay in southeastern Australia. Cushing (1983) concluded that fish larvae were generally too few to affect the density of their prey, but that this would be likely to change after metamorphosis. However, a recent simulation of larval fishes and their prey indicated that larval fish can affect prey density

(Bollens 1988). In a study of tuna larvae from tropical waters, we found evidence of larvae competing for food, which resulted in a density-dependent reduction in their growth rate. Such density-dependence would have important consequences for the survivorship of the larval population (Young and Davis 1990, Jenkins et al. 1991).

Since 1985, a fishery has been established for jack mackerel, *Trachurus declivis*, in the waters of eastern Tasmania (Williams et al. 1987). As this fishery has developed, so has the need to understand more about the biology of this fish, particularly its early life history. The diet of larval *T. declivis* has not been examined previously. However, the diet of larvae of the closely related *T. symmetricus* has been studied in California Current specimens (Arthur 1976), and of *T. mediterraneus* in Black Sea specimens (Sinyukova 1964). Both studies reported that the larvae ate mainly copepods, and occasionally other taxa including euphausiid larval stages. Arthur indicated that *T. symmetricus* selected for the harpacticoid copepod *Microsetella norvegica*. Neither study reported diel feeding cycles in the larvae of these *Trachurus* species.

Larvae of *Trachurus declivis* are present during summer in coastal waters surrounding Tasmania (A. Jordan, Tasmanian Department of Sea Fisheries, personal communication). The productivity of these waters is strongly influenced by the relative position of subtropical and subantarctic water masses in the vicinity. Generally, the greater the contribution of subantarctic water the higher the productivity (Harris et al. 1991). In years of low productivity, small zooplankters (particularly small copepods) dominate and large zooplankters such as the euphausiid *Nyctiphanes australis* are largely absent, whereas in years of high productivity this pattern is largely reversed (Harris et al. 1991). Such variation in the zooplankton community will obviously affect the prey available to larval *T. declivis* from year to year.

The purpose of the present study was twofold. The first aim was to describe aspects of the feeding of larval *Trachurus declivis* from coastal waters of east Tasmania. The second was to assess the impact of larval *T. declivis* on prey populations.

Materials and methods

Field collections

Larvae were collected at a fixed position in Storm Bay (43° 10'S; 147° 31'E Fig. 1) and from the east coast of Tasmania in the area of Maria Island in the summers of 1988, 1989 and 1990 to examine gut contents (Table 1). Two specific larval collections were also made during this time. In January 1989, larvae collected along the coast of eastern Tasmania were used to examine the relationship between feeding success and zooplankton biomass (Fig. 1). Data on diel feeding was obtained from collections made between 14 and 16

Table 1. *Trachurus declivis*. Number of larvae examined for gut contents. Larvae from east coast were all collected around Maria Island, except for the 203 larvae collected in January 1989. nd: no data

Date	Storm Bay	East coast
1988		
Jan.	53 ^a	nd
1989		
Jan.	40 ^a	155
Jan.		203 ^b
Feb.	60	20 ^a
Mar.	nd	17
1990		
Feb.	nd	216 ^{a,c}
Total (764)	153	611

^a Larvae used to examine prey selection

^b Larvae collected from stations along east coast of Tasmania to examine relationship between feeding success and available prey, but not used in dietary analyses

^c Larvae used to examine diel feeding

February 1990 from Riedle Bay, Maria Island (Fig. 1). Samples were collected at ~2 h intervals, and at ~1 h intervals from 15.00 to 22.30 hrs, to estimate gut-evacuation rates.

Larvae were collected from Storm Bay by the CSIRO's inshore research vessel F.R.V. "Scottsman". Oblique tows were made through the mixed layer to ~25 m depth with a 1 m ring net of 500 µm mesh netting towed at 1 m s⁻¹. Tow depth was estimated from metres of wire out. Larvae were sampled off east Tasmania from the Tasmanian Sea Fisheries research vessel "Challenger" with paired bongo nets (50 cm mouth diam; 500 µm mesh netting) to 30 m depth. Depth was determined with a salinity-depth recorder. Larvae for the diel study were collected with a 70 cm ring net of 500 µm mesh netting towed at 1 to 2 m s⁻¹ from F.R.V. "Scottsman". Storm Bay samples were fixed in 4% formalin buffered with borax. All samples from the east coast were fixed in 95% alcohol to preserve the otoliths (A. Jordan personal communication). According to Theilacker (1980), larval *Engraulis mordax* preserved in formalin shrink by ~10% of live standard length, whereas shrinkage in alcohol is negligible. However, as shrinkage of larval *Trachurus declivis* has not as yet been examined, we present our data here on the unadjusted lengths.

Immediately after each zooplankton tow, microplankton were collected from Storm Bay with drop nets (Heron 1982) of 37 µm mesh netting (mouth diam = 50 cm) to a depth of 40 m. Drop nets were also used to collect microzooplankton from the east coast. However, collections were less systematic on the east coast, but sufficient samples were collected to examine prey selection. All microplankton samples were preserved in 4% buffered formalin.

Larvae were identified following an unpublished guide (D. Furlani, CSIRO, unpublished data). There are difficulties in separating larvae of *Trachurus declivis* from larvae of the closely related *T. novaezelandiae* (D. Furlani personal communication). However, the area in which the larvae were collected supports a large fishery for *T. declivis* (Williams et al. 1987). Also, despite the large number of fish collections made in the area, there have been no positive records of *T. novaezelandiae* (P. Last, CSIRO, personal communication).

Hydrographic data were obtained from the CSIRO Storm Bay master station (43°11'S, 147°32'E) (Clementson et al. 1989), and from the continuous records of the CSIRO coastal monitoring station off Maria Island (42°36'S; 148°16'E) (Harris et al. 1987).

Laboratory analysis

In samples that contained less than 30 larvae, all individuals were dissected; in larger samples, a random subsample of 30 to 50 larvae was taken. The larvae were measured in glycerine under a stereomicroscope. Standard length (SL) and mouth width were measured according to Young and Davis (1990), although distortion of the mouth in many larvae meant that mouth width could not always be measured. Stomach contents were teased from the stomach with 0.25 mm tungsten needles electrolytically sharpened for the purpose. The contents were identified to species where possible, measured along the widest axis, and counted. Chlorazol Black e was added to the glycerine to aid identification of Crustacea. Stomach fullness was estimated on a scale of 1 to 5 (1, empty; 2, < half full; 3, ~half full; 4, > half full; 5, full). The stage of digestion was estimated on a scale of 1 to 3 (1, digested; 2, partially digested; 3, contents intact).

Not all 500 µm-net samples contained larvae, and of these fewer contained sufficient numbers to enable useful comparisons with the accompanying microzooplankton samples. Therefore, for the prey selection study we randomly selected microzooplankton samples from both Storm Bay and the east coast where the accompanying 500 µm net sample had >20 larvae. The numbers of microzooplankton were estimated after initially filtering plankton samples through a 1 mm screen to exclude zooplankters of a larger size than that eaten by the larvae (J. Young unpublished data). Five aliquots were taken with a stempel pipette (1/40 of the total vol-

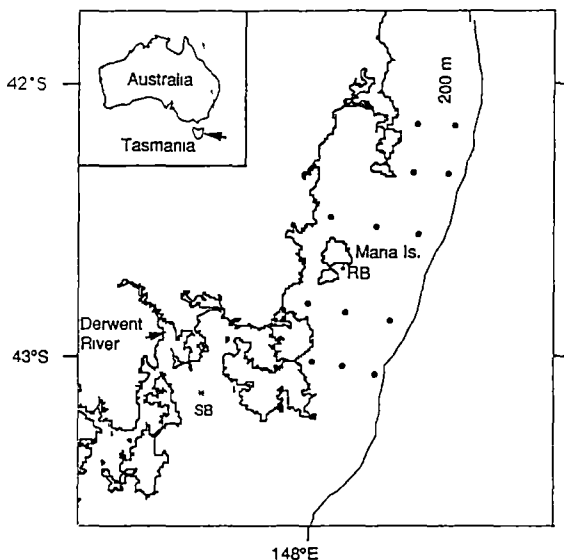


Fig. 1. Location of sampling stations for *Trachurus declivis* larvae around eastern Tasmania, Australia. SB: Storm Bay master station; RB: Riedle Bay; ●: stations from which larvae were compared with biomass of zooplankton

ume = 5 ml), and the microzooplankton were sorted into major prey groupings and counted. Only taxa eaten by the larvae were counted. To examine whether feeding success was related to zooplankton availability, displacement volumes (expressed as ml 100 m⁻³) were measured for the zooplankton fraction collected by 500 µm nets from east coast stations (see Fig. 1).

Data analysis

The relationship between feeding incidence and standard length was examined using a test for linear trends in the proportion of larvae with food as a function of larval length (Kirkwood 1988). The relative importance of prey items was determined from the product of percent frequency of occurrence and percent number (Laroche 1982). Diet breadth (B) was calculated for larvae from different areas using Levins' (1968) index, $B = (\sum p_i^2)^{-1}$, where p_i is the proportion of each prey category in the diet. Values were standardised to fractions using Hespeneheide's (1975) transformation, $B_s = (B-1)/(n-1)$, where n is the number of prey categories.

Diel changes in feeding were examined for larvae collected between 14 and 16 February 1990. Differences in feeding intensity in larvae between the morning (07.00 to 10.00 hrs), midday (10.01 to 14.00 hrs) and afternoon (14.01 to 20.00 hrs) were examined using ANOVA on the $\sqrt{(x+1)}$ number of prey larva⁻¹. Differences in stomach fullness and state of digestion with time of day were examined using contingency tables. The number of larvae caught per tow was low during this period (mean = 10.3, SE = 2.3). Therefore, as weather conditions were the same over the two days, we assumed that larvae collected at the same time but on different days were directly comparable.

Prey selection was examined in larvae taken from Storm Bay, and from a station off Maria Island, each at two different times. Pearre's C index (Eq. 3, p. 915 in Pearre 1982) was used, since it has most of the characteristics of the "ideal" selectivity index (Lechowicz 1982). Selectivity indices were calculated separately for larvae ≤ 6 mm and > 6 mm SL, and were based on the pooled diet of at least ten larvae. Sample sizes smaller than this were considered insufficient to assess prey selection accurately. Gut evacuation time and rate (R) were calculated from the regression of prey number and time from last feeding. Daily ration (C_t) was calculated using Elliott and Persson's (1978) formula,

$$C_t = \frac{(S_t - S_0 e^{-Rt}) \cdot Rt}{1 - e^{-Rt}},$$

where S_0 and S_t are stomach contents at the beginning and end of time t .

Results

Physical environment

Sea surface temperatures in the study area ranged between 11 and 19.5°C over the three years, although during the spawning period of *Trachurus declivis* (January to March, A. Jordan unpublished data) temperatures were between 16.5 and 19.5°C (Fig. 2). Surface temperatures were ~2°C higher in the summer of 1988/1989 than in the preceding and following summers due to the intrusion of subtropical water into the area [Fig. 2 and see Harris et al. (1991)]. Harris et al. (1991) reported that salps and *Nyctiphanes australis* were present during the 1987/1988 summer, but were absent the following summer (1988/1989) when the subtropical intrusion was most pronounced. No discernible difference in temperature was

detected between our two areas. However, the surface waters of Storm Bay were slightly less saline during summer than those off Maria Island, presumably due to freshwater runoff from the Derwent and Huon Rivers (Fig. 2).

Feeding incidence

The gut contents of 561 larval *Trachurus declivis* from Storm Bay and eastern Tasmania were examined (Table 1). A further 203 larvae were examined for feeding incidence, but their prey were not identified. The Storm Bay larvae ranged in size from 2.4 to 13.3 mm SL [mean 5.0 (±0.2 SE) mm SL], although most (~70%) were between 3.5 and 5 mm SL (Fig. 3). Larvae from the east coast ranged in size from 3.3 to 20.4 mm SL [mean 6.1 (±0.1 SE) mm SL], and were significantly larger than those from Storm Bay (Student's t -test, DF = 460, $P < 0.001$; Fig. 3). In all, 78.0% of the guts examined from daytime (06.30 to 20.00 hrs) samples contained food (81.0% of Storm Bay larvae; 77.2% of east coast larvae). Of the larvae taken at night (20.00 to 06.00 hrs) only 38% contained food, the majority of which was digested. Only one stomach contained food (also digested) after midnight. There was a positive linear relationship between feeding incidence (percentage of stomachs containing food) and larval size in larvae caught during daytime from Storm Bay ($\chi^2 = 14.3$, DF = 5, $P = 0.0001$;

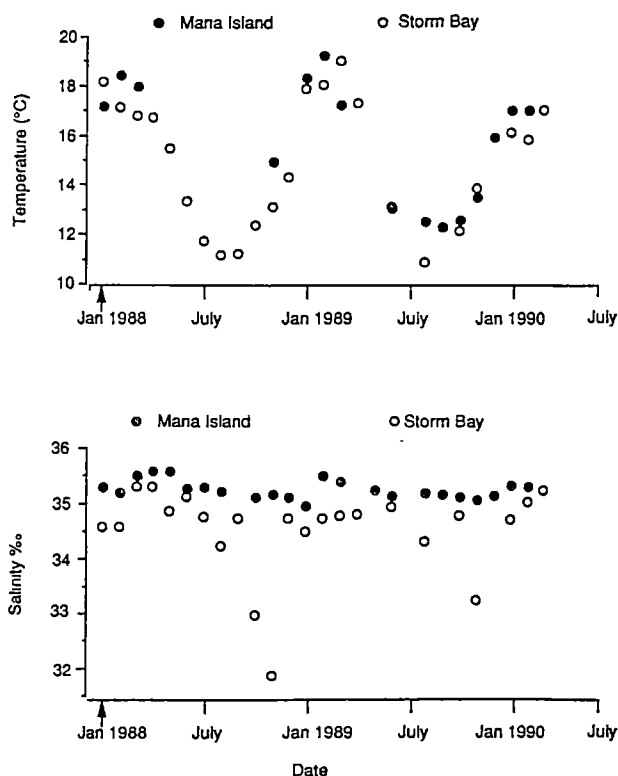


Fig. 2. Monthly sea surface temperature (a) and salinity (10⁻³) (b) from the Storm Bay master and Maria Island monitoring stations between January 1988 and March 1990

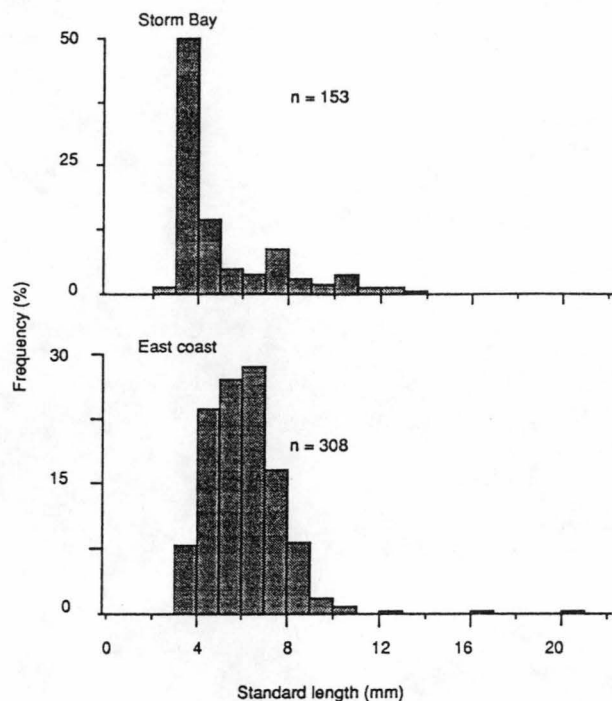


Fig. 3. *Trachurus declivis*. Length-frequency distribution of larvae examined for gut contents from Storm Bay and east coast of Tasmania

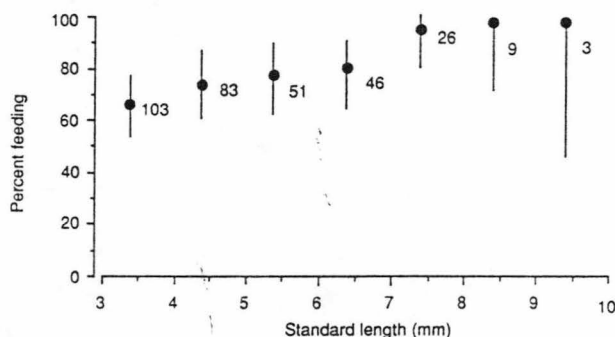


Fig. 4. *Trachurus declivis*. Relationship between feeding incidence and standard length in larvae from eastern Tasmania; means \pm 95% confidence limits. Values beside data points show number of larvae examined

Fig. 4). No relationship was found between feeding incidence and zooplankton biomass in 500 μ m nets taken along the coast of eastern Tasmania.

Overall diet and interannual variability

The larvae of *Trachurus declivis* fed largely on crustacean microzooplankton, although bivalve veligers (*Mya* spp. and *Pecten* spp.) were identified in the guts of some east coast larvae. The harpacticoid *Microsetella rosea*, *Oithona* spp., species of calanoid copepods (mainly *Clausocalanus furcatus* and *Paracalanus aculeatus*), copepod

Table 2. *Trachurus declivis*. Summary of prey items in larvae ($n=153$) from Storm Bay [size range, standard length (SL) = 2.35 to 14.25 mm, mean = 5.07 ± 0.20 (SE) mm]. The product ($F \cdot N$) of frequency of occurrence (F) and percentage number (N) of each prey type is measure of importance of each prey type. Range shows number of prey in individual larvae

Prey taxon	<i>F</i>	<i>N</i>	<i>F</i> · <i>N</i>	Range
Cladocera				
<i>Podon intermedius</i>	0.76	0.20	0.15	0–1
Copepoda				
Harpacticoida				
<i>Euterpina acutifrons</i>	0	0	0	0
<i>Microsetella rosea</i>	25.00	10.78	269.50	0–4
Cyclopoida				
<i>Oithona</i> spp.	23.48	22.16	520.32	0–13
<i>Oncaea venusta</i>	5.30	1.40	7.42	0–1
Calanoida				
<i>Acartia</i> spp.	0.76	0.20	0.15	0–1
<i>Acrocalanus</i> spp.	0.76	0.20	0.15	0–1
<i>Calanoides caranatus</i>	0	0	0	0
<i>Calanus</i> spp.	1.52	0.40	0.61	0–1
<i>Clausocalanus furcatus</i>	8.33	4.19	34.90	0–4
<i>Cosmocalanus darwinii</i>	1.52	0.20	0.30	0–1
<i>Neocalanus robustior</i>	1.52	0.80	1.22	0–3
<i>Paracalanus aculeatus</i>	3.79	1.20	4.55	0–2
unidentified calanoids	18.18	8.18	148.71	0–4
eggs	9.85	4.39	43.24	0–4
nauplii	46.21	19.16	885.38	0–5
copepodites	4.55	2.79	12.69	0–5
Caridea				
unidentified juveniles	0	0	0	0
Euphausiacea				
<i>Nyctiphanes australis</i> (calyptopis stage)	28.03	23.15	648.89	0–12
Decapoda				
crab zoea	0	0	0	0
Bivalvia				
<i>Mya</i> spp.	0	0	0	0
<i>Pecten</i> spp.	0	0	0	0
Unidentified	3.03	0.80	2.42	0–1

nauplii and calyptopis stage larvae of *Nyctiphanes australis* were the main prey (Tables 2 and 3). Algae were not observed in the stomachs of any larvae.

The relative proportions of prey differed between larvae from Storm Bay (Table 2) and those from eastern Tasmania (Table 3). The diet of Storm Bay larvae was dominated by copepod nauplii, calyptopis stage *Nyctiphanes australis* (only during the 1988 season), *Microsetella rosea*, *Oithona* spp. and calanoids. In contrast, the eastern Tasmanian larvae ate chiefly *M. rosea*, *Oithona* spp., *Oncaea venusta* and *Paracalanus aculeatus*. Very few *N. australis* were eaten by east coast larvae, and only during the 1990 season. It was not possible to gauge the relative dietary importance of individual calanoid species because of the poor condition in which most were found. However, their continual occurrence indicated that they were generally important, particularly in larvae from the east coast.

Table 3. *Trachurus declivis*. Summary of prey items in larvae ($n=308$) from eastern Tasmania [size range SL=3.26 to 20.44 mm, mean = 6.09 ± 0.10 (SE) mm]. The product ($F \cdot N$) of frequency of occurrence (F) and percentage number (N) of each prey type is measure of importance of each prey type. Range refers number of prey in individual larvae

Prey taxon	F	N	$F \cdot N$	Range
Cladocera				
<i>Podon intermedius</i>	9.09	5.63	51.18	0–4
Copepoda				
Harpacticoida				
<i>Euterpina acutifrons</i>	1.36	0.50	0.68	0–1
<i>Microsetella rosea</i>	48.64	36.42	1 771.47	0–8
Cyclopoida				
<i>Ouhona</i> spp.	12.27	6.13	75.22	0–3
<i>Oncaea venusta</i>	14.09	8.94	125.96	0–10
Calanoida				
<i>Acartia</i> spp.	0.91	0.33	0.30	0–1
<i>Acrocalanus</i> spp.	0	0	0	0
<i>Calanoides caranatus</i>	0.45	0.17	0.08	0–1
<i>Calanus</i> spp.	0	0	0	0
<i>Clausocalanus furcatus</i>	7.27	3.15	22.90	0–2
<i>Cosmocalanus darwinii</i>	0.91	0.33	0.30	0–1
<i>Neocalanus robustior</i>	0.45	0.17	0.08	0–1
<i>Paracalanus aculeatus</i>	9.09	8.94	81.26	0–16
unidentified calanoids	32.73	17.55	574.41	0–9
eggs	1.36	0.50	0.68	0–1
nauplii	10.91	4.53	49.42	0–3
copepodites	2.73	1.82	5.00	0–4
Caridea				
unidentified juveniles	0.91	0.33	0.30	0–1
Euphausiacea				
<i>Nyctiphanes australis</i> (calyptopis stage)	5.91	2.32	13.71	0–2
Decapoda				
crab zoea	0.45	0.33	0.15	0–2
Bivalvia				
<i>Mya</i> spp.	0.45	0.17	0.08	0–1
<i>Pecten</i> spp.	0.91	0.66	0.60	0–3
Unidentified remains	1.45	0.54	0.78	0–1

Table 4. *Trachurus declivis*. Interannual variability in mean prey number and rank order (1–6) of importance (based on $F \cdot N$) of major prey taxa in larvae from Storm Bay and east coast of Tasmania. Values in parentheses are: no. of larvae; mean prey no. per larva \pm SE. –: no euphausiids present

Prey taxon	Storm Bay		East coast	
	1988 (53; 7.17 ± 0.74)	1989 (100; 1.25 ± 0.13)	1989 (192; 1.85 ± 0.15)	1990 (216; 2.14 ± 0.27)
Cladocera	6	–	4	6
Harpacticoida	4	2	1	2
Cyclopoida	2	3	2	3
Calanoida	1	3	3	1
Calanoid	5	1	5	5
nauplii				
Euphausiacea	3	5	–	4

The relative importance of major prey taxa differed between years (Table 4). In 1988 larvae from Storm Bay ate mainly cyclopoids, calanoids and euphausiids, whereas in 1989 harpacticoids, cyclopoids and calanoids were the chief prey taxa. Only two larvae sampled in 1989 had euphausiids in their stomachs. East coast larvae ate primarily the harpacticoid *Microsetella rosea*, cyclopoids and calanoids in 1989. Euphausiids were absent as prey during that time. In 1990 calanoids, followed by harpacticoids and cyclopoids were the main prey.

Numbers of prey

The number of prey items per larva ranged from 0 to 28. Fewer numbers of prey were eaten by larvae in Storm Bay in 1989 than in 1988 (Student's t -test, $DF=151$, $t=10.49$, $P=0.0001$; Table 4). Mean prey number in east coast larvae was not significantly different between 1989 and 1990 (t -test, $p>0.1$). A comparison of prey number between larvae sampled in 1989 from Storm Bay and the east coast (when larvae were sampled concurrently) showed no significant difference in prey number (t -test, $P>0.1$; Table 4). Number of prey was positively correlated with standard length in Storm Bay (Fig. 5). The relationship was less clear in east coast larvae, which may reflect the relatively higher numbers of larger-sized calanoids.

Diet breadth

Diet breadth was low in larvae from Storm Bay (Table 5), where diets were dominated by either *Microsetella rosea*

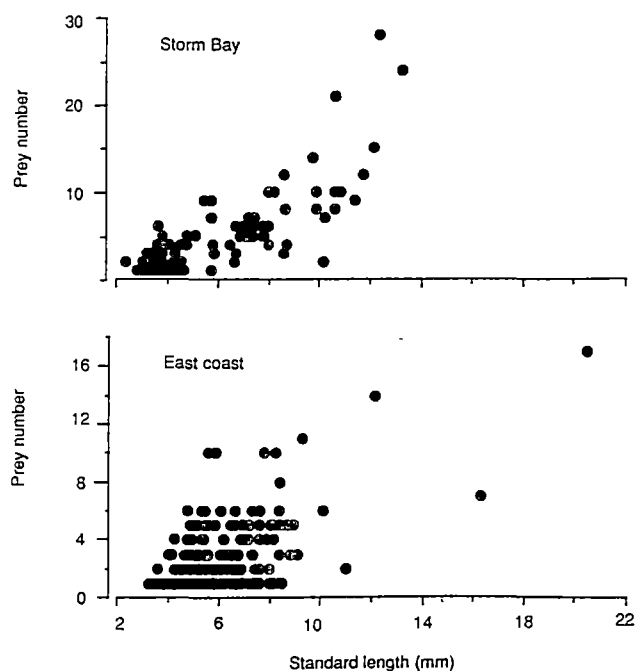


Fig. 5. *Trachurus declivis*. Relationship between prey number and standard length in larvae from Storm Bay and east coast of Tasmania

Table 5. *Trachurus declivis*. Diet breadths, calculated using Levins' (1968) index, of larvae from Storm Bay and the east coast (number of larvae in parentheses)

Area	Length class (mm)			
	≤4.0	4.0–6.0	6.01–8	8.01 +
Storm Bay	0.11 (82)	0.18 (35)	0.29 (39) ^a	
Maria Island	0.53 (21)	0.14 (135)	0.37 (120)	0.21 (32)

^a Length classes combined

or copepod nauplii. Diet breadth increased slightly in larger larvae due to the presence of calyptopis stage *Nyctiphanes australis*. The east coast larvae, particularly those ≤4 mm, had more broadly based diets (Table 5).

Changes in diet with size

The relationship between mouth width (mw) and standard length (SL) was allometric, of the form $mw = 0.086 SL^{1.055}$ ($r^2 = 0.87$, $DF = 62$, $P = 0.0001$). Mouth width was positively correlated with prey width (Fig. 6), and was always larger than the largest prey width measured. The ratio between maximum prey width to mouth width ranged from 1.5 to 1.8, but did not differ with size of larvae. Generally, as the size of larvae increased there was a progression from smaller to larger prey taxa. In Storm Bay, copepod nauplii were the main prey taxa of larvae ≤4 mm SL. Their importance decreased in larger-sized larvae, the diets of which were increasingly dominated by the harpacticoid *Microsetella rosea*, calanoids and calyptopis stage *Nyctiphanes australis* (Fig. 7). Off eastern Tasmania, copepod nauplii were also the main prey item of larvae ≤4 mm. The diets of larger larvae, particularly those ≥8 mm, were increasingly dominated by cyclopoids (mainly *Oithona* spp.) and calanoid copepods. However, calyptopis stage *N. australis* were less common in the east coast larvae (Fig. 7), while the cladoceran *Podon* spp., rarely present in the diet of Storm Bay larvae, was found in larger-sized larvae from the east coast.

Prey selection

There was significant variation in the (arcsine-transformed) proportions of prey taxa collected from drop nets between stations (ANOVA, $F = 3.43$, $DF = 27$, $P = 0.012$), and this was reflected in the relative importance of prey taxa in the diet. However, general patterns of prey selection were evident between stations (Fig. 8). The strongest patterns to emerge were selection for the harpacticoid *Microsetella rosea* and selection against calanoids in both Storm Bay and east coast larvae (Fig. 8), even though calanoids were an important prey item. These patterns were generally reflected by the prey-selection indices (Table 6), although different prey preferences were noted for small (≤6 mm SL) and larger (>6 mm SL) larvae. Selection against *M. rosea* by larvae >6 mm from the Storm Bay station on 15 January 1988

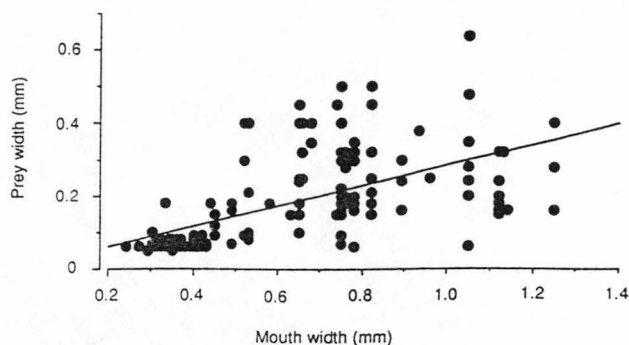


Fig. 6. *Trachurus declivis*. Relationship between mouth width of larvae and prey width

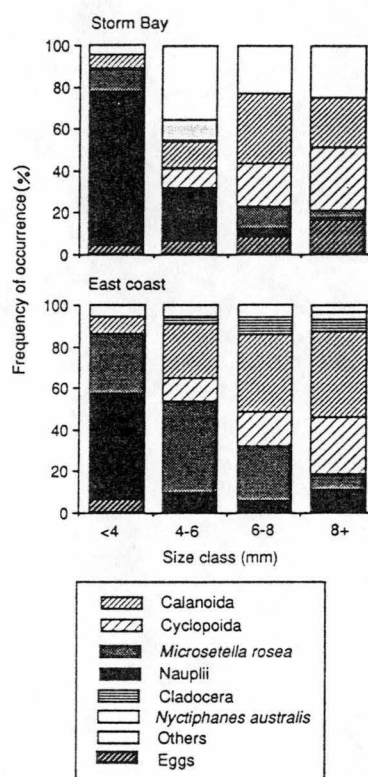


Fig. 7. *Trachurus declivis*. Frequency of occurrence of major prey taxa in relation to size of larvae from Storm Bay and east coast of Tasmania

may have occurred because these were, on average, significantly larger (mean $7.42 \text{ mm} \pm 0.20 \text{ SE}$) than the other larvae >6 mm from the other stations examined (mean $6.64 \text{ mm} \pm 0.14 \text{ SE}$) (ANOVA, $F = 3.60$, $DF = 47$, $P < 0.05$). Cyclopoids were selected against by larvae ≤6 mm, whereas positive selection was noted in larvae >6 mm. Generally, calanoids were selected against by both size classes. Larvae ≤6 mm selected for copepod nauplii, whereas larger larvae selected against this taxon. Also noted was selection for euphausiids (*Nyctiphanes australis*), when they were present, by both size classes of

Table 6. *Trachurus declivis*. Values of Pearre's C index for larvae \leq or > 6.0 mm SL feeding on major prey taxa from Storm Bay (SB) and Maria Island (MI). Positive values show selection for, and negative

values show selection against, a particular prey taxon. (n): No. of larvae. *, **: Selection significant at $P < 0.05$, and $P < 0.01$, respectively. -: Insufficient data for comparison

Station/month/ year (n)	Prey taxa (size in mm)									
	Harpacticoida		Cyclopoida		Calanoida		Euphausiacea		Nauplii	
	≤ 6.0	> 6.0	≤ 6.0	> 6.0	≤ 6.0	> 6.0	≤ 6.0	> 6.0	≤ 6.0	> 6.0
SB 15/1/88 (50)	+0.43**	-0.52**	-0.24**	+0.10*	-0.18**	+0.06	+0.22**	+0.31**	-0.04	-0.40**
SB 15/2/89 (30)	+0.38**	-	-	-	-0.07	-	-	-	+0.40**	-
SB 24/2/89 (30)	+0.45**	-	-	-	-0.13*	-	+0.22**	-	+0.57**	-
MI 24/1/89 (30)	+0.37**	+0.26**	-	-	-0.22**	-0.15*	-	-	+0.01	-
MI 28/2/89 (20)	-	+0.17*	-	+0.26*	-	-0.19*	-	-	-	-0.33**

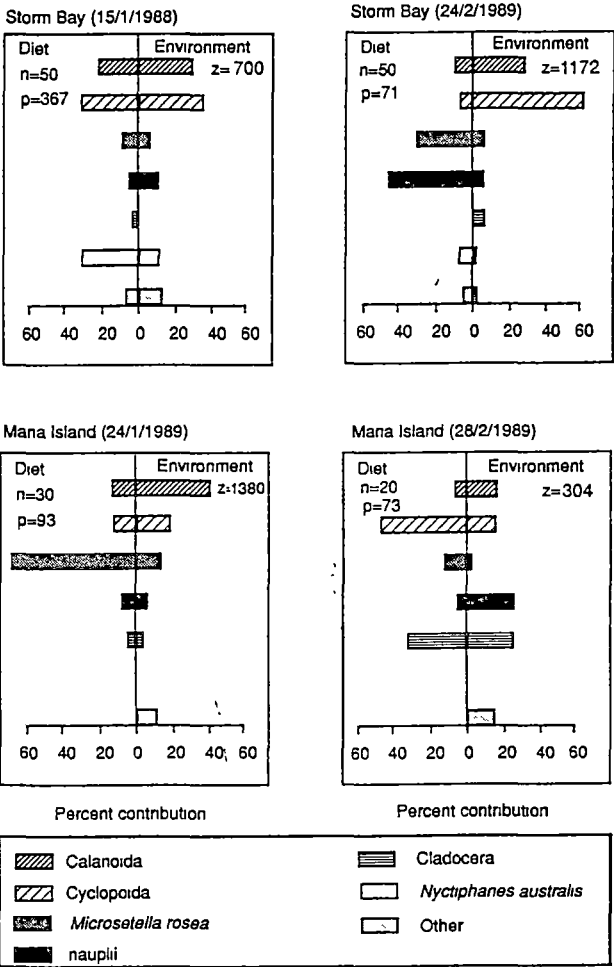


Fig. 8. *Trachurus declivis*. Comparison between relative proportions of prey in diet of larvae with those of their prey in environment of Storm Bay master station and Riedle Bay, Maria Island, on two different occasions. n: number of larvae examined; p: total number of prey identified in larvae; z: number of prey m^{-3} in water column

larvae. The presence of later-staged furcilia of *N. australis* in the stomachs of larger larvae indicated size selection within this taxon. The presence of cladocerans (*Podon* spp.) usually reflected their relative abundance in the environment.

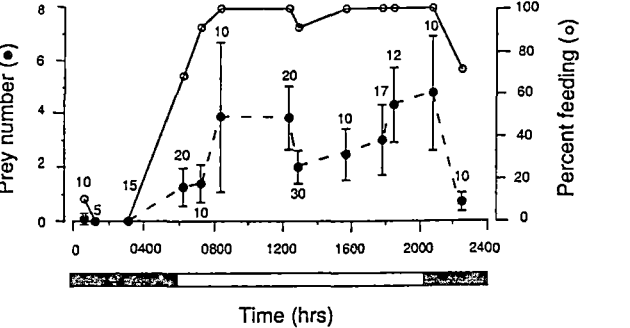


Fig. 9. *Trachurus declivis*. Feeding in relation to time of day. Data show mean prey number larvae $^{-1}$ station $^{-1}$ \pm 95% CL and percent of larvae feeding at each station. Values beside data points show number of larvae examined. Shaded portion of time bar indicates night

Diurnal feeding

Larvae fed only during daylight hours (Fig. 9), and ate significantly less in the middle of the day than in either the morning or afternoon (ANOVA, $DF = 221$, $F = 14.4$, $P = 0.0001$). Correspondingly, stomach-fullness values were higher in the morning and late afternoon than in the middle of the day ($\chi^2 = 27.01$, $DF = 8$, $P = 0.0001$). Prey were less fully digested at these times ($\chi^2 = 20.1$, $DF = 4$, $P = 0.0005$), which also indicated recent ingestion.

Gut evacuation and daily ration

Stomach-fullness values rose to their highest at around 20.00 hrs (Fig. 9). Regression of prey number with time after 20.00 hrs gave a digestion time of ~ 6 h ($y = -0.005x + 13.729$, $r^2 = 0.44$, $F = 33.06$, $DF = 43$, $P = 0.0001$) at a water temperature of $18^\circ C$. However, Fig. 9 suggests that the major portion of gut contents are evacuated in about 4 h. Two feeding peaks, one in the morning and one in the afternoon, indicate that larvae feed at least twice per day. The daily ration was estimated, using the equation of Elliott and Persson (1978), at between 5 and 10 prey larvae $^{-1}$ d $^{-1}$, depending on the size of the larvae (Table 7). After conversion of prey size to dry weight for copepods (Hunter 1981), the amount eaten was estimated to range from 26 μg dry wt larva $^{-1}$ d $^{-1}$ in larvae ≤ 6 mm

Table 7. *Trachurus declivis*. Estimates of daily ration for larvae \leq or >6 mm SL. dw: dry weight equivalent of prey, in μg ; %DR: daily ration as percentage of larval body wt

Size category	Mean length (SL, mm)	Dry weight (mg)	Mean prey d^{-1} (dw)	%DR
≤ 6 mm SL	4.40 (± 0.05 SE)	0.186	5.09 (25.5)	13.7
> 6 mm SL	7.66 (± 0.13 SE)	0.840	9.79 (78.3)	9.3

to 78 μg in larvae >6 mm. From the relationship between standard length and dry weight of larval *Trachurus declivis* (dry wt = $0.334 \text{ SL} - 1.38$, $r^2 = 0.71$, $\text{DF} = 19$, $F = 44.0$, $P = 0.0001$), we calculated that the larvae ate daily between 9 and 13% of their body weight in food.

Discussion

Feeding incidence

The incidence of food in the guts was high in larvae from both Storm Bay and the east coast, and was similar to that found in *Trachurus symmetricus* from the California Current (Arthur 1976). High feeding incidence has previously been associated with a looped gut, as this reduces the amount of regurgitation on capture (Arthur 1976). In *T. declivis* the gut loops at about 3.5 mm SL (J. Young personal observation), which is approximately the size at which the larvae begin to feed. However, not all larvae had food in their stomachs. This was probably due to larval size – we found a positive relationship between size and feeding incidence. Both feeding success and the subsequent condition of larval fishes have been correlated with zooplankton biomass (Arthur 1976, Koslow et al. 1985, Young and Davis 1990). In the present study, however, no relationship was found between feeding and zooplankton biomass, indicating that the larvae were not food-limited, although the use of 500 μm nets to collect zooplankton restricts this conclusion (Frank 1988).

Overall diet and interannual variability

Copepods, particularly the harpacticoid *Microsetella rosea* and the cyclopoid *Oithona* spp., are the major component of the diet of larval *Trachurus declivis*, as they are in the diet of *T. symmetricus* and *T. mediterraneus* larvae (Sinyukova 1964, Arthur 1976). Of interest was the presence of larval bivalves, particularly larvae of *Pecten* spp., in the diet of some larvae. *Pecten* spp. supported an important fishery in the area until fishing pressure forced its closure (Young and Martin 1989). However, as they are not readily digested, and are of little nutritional value (Checkley 1982, Schnack 1974), it is unlikely that they are an important prey item.

The presence of larval euphausiids in the diet of larval fishes has been reported previously (e.g. Arthur 1976, Tully and Ceidigh 1989). However, the importance of the

euphausiids in some of our samples is noteworthy. *Nycetiphanes australis* is a key member of the zooplankton community in Tasmanian coastal waters (Ritz and Hosie 1982), where it is the main component of the diet of adult jack mackerel (Webb 1976). Adult jack mackerel have been fished commercially in these waters since 1985 (Williams et al. 1987). A downturn in catches in the 1988–1989 summer fishing season corresponded with the disappearance of *N. australis* from inshore waters of southeastern Tasmania (Harris et al. 1991). Of the three summers in which we collected fish larvae, larval *N. australis* was present as prey only during the summers of 1987/1988 and 1989/1990, which mirrored their presence in the plankton (Harris et al. 1991). Harris et al. (1991) found that intrusions of nutrient-low subtropical water during the 1988/1989 summer led to a downturn in local productivity and the disappearance of “large” zooplankters such as *N. australis* which they propose relies on new productivity. They found that the biomass of small copepods, which can switch from herbivory to omnivory (Cushing 1989), was less affected by changes in production during the same period. This response is mirrored in the diet of the larvae, as the small copepods (e.g. *Microsetella rosea* and *Oithona* spp.) were particularly prevalent in the larvae from the 1988/1989 summer. However, the lower prey numbers during this period in both the Storm Bay and east coast larvae suggests that the production of copepods may also have been affected.

Comparison between areas

Govoni and Chester (1990) found that the diet of larval spot, *Leiostomus xanthurus*, differed between adjacent water masses at the mouth of the Mississippi River. They proposed that differences in both the abundance of food organisms and the photic environment were responsible. In the present study, differences in both the number and relative importance of prey types were noted (see Table 4). Whether these differences were the result of the fine-scale physical oceanography of the area is difficult to tell, as the hydrography of the waters surrounding eastern Tasmania is complex (Harris et al. 1987). The waters off Maria Island lie at the junction of subantarctic and subtropical waters. Storm Bay, on the other hand, is affected not only by both subantarctic and subtropical waters, but also receives a significant input from the Derwent and Huon Rivers (Clementson et al. 1989). The extent to which these differences in water-mass structure affect local prey distributions has yet to be resolved. Further work on the plankton of these areas is needed.

Size and prey selection

Prey size is a critical factor in prey selection by most fish larvae (e.g. Schmitt 1986, Theilacker 1987), the size selected being largely determined by the gape of the mouth and the width of the prey (Last 1980). As the larva grows, the proportion of larger items in the diet increases, helping to meet the larva's increased energetic requirements

(Hunter 1981). Such a progression in prey size may also reduce intraspecific competition between larval size classes (Shelbourne 1962). Larval *Trachurus declivis*, for example, ate largely nauplii when <4 mm SL, but as they grew began eating larger prey such as calanoids and euphausiid larvae. A similar shift in diet has been reported for *T. symmetricus* (Arthur 1976), and for many other larval fishes (see review in Theilacker and Dorsey 1980). However, in the present study some larger larvae were full of large numbers of smaller prey (e.g. *Microsetella rosea*), apparently obtaining sufficient food from them. Therefore, even though predator mouth width limits the upper size boundary of prey (width) eaten, larger larvae are quite capable of obtaining sufficient food from smaller prey types. Larval jack mackerel fed small food items (*Gymnodinium* spp.) in the laboratory were as healthy, and grew as fast, as those fed on larger prey (Theilacker and Dorsey 1980).

Many larval fishes are opportunistic feeders, taking prey in direct proportion to their abundance in the environment (Stepien 1976), the dominant food type varying with its seasonal abundance in the plankton (Last 1978, 1980). To some extent the larvae of *Trachurus declivis* follow this pattern, their diet changing with changes in the distribution and abundance patterns of zooplankton in the area (Harris et al. 1991). However, selection for certain prey taxa was apparent. For example, the positive selection for *Microsetella rosea* found in the present study mirrors the selection of *M. norvegica* by *T. symmetricus* in the northern hemisphere (Arthur 1976). Possibly the bright colouration of such harpacticoid species attracts these predators (Arthur 1976).

Diurnal feeding

The pattern of feeding of larval *Trachurus declivis* is typical of most marine larvae: larvae fed during the day, with peaks in feeding in the early morning and late afternoon (e.g. Last 1978, 1980, Young and Davis 1990). This trait appears to be the precursor of adult feeding behaviour, as feeding peaks in the morning and afternoon have been reported in adult *T. declivis* (Shuntov 1969). Some fish larvae, particularly larval plueronectiforms, feed during the night (Blaxter 1969, Sumida and Moser 1980, Jenkins 1987, Watson and Davis 1989). However, most fish larvae are visual feeders (Hunter 1981), and it may be that some reported instances of night feeding reflect slow digestion times (Watson and Davis 1989), although moonlight feeding is possible (Last 1978). The apparently high feeding incidence after sunset in the present study can be attributed to the presence of undigested prey. We estimated that digestion in this species takes around 4 h. Empty stomachs were not found until 1 h after midnight, 5 h after sunset.

Digestion, daily ration and predatory impact

Our estimate of digestion time is based on the assumption that feeding ceased at dark. This assumption was sup-

ported by the presence of increasingly digested material in the guts after sunset. Estimating gut-evacuation rates from field samples is obviously not as accurate as direct measurement in the laboratory; however, comparative studies indicate that field estimates are reasonable. For example, the rate for *Engraulis mordax* in the laboratory (1.15 to 2.73 h; Theilacker 1987) was very similar to that estimated in the field (1 to 3 h; Arthur 1976). The rate of digestion we found in the present study is similar to that of larvae of other temperate-water fishes (see Govoni et al. 1986). For example, gut evacuation in *Rhombosolenia tapirina* from temperate waters of southeastern Australia takes 4 h (Jenkins 1987). *Scomber japonicus* completes digestion over about 7 h, at a water temperature of 19°C (Hunter and Kimbrell 1980). Our results contrast with those of Peterson and Ausubel (1984), who found that digestion in *S. scombrus* takes 1 to 2 h.

The density of *Trachurus declivis* ranged from 0 to a maximum of 4 larvae m⁻³ (A. Jordan unpublished data) around Maria Island. However, the median value was ~0.05 larvae m⁻³ in 1989 and even lower in 1990 (0.01 larvae m⁻³). Each larva, depending on size, can eat between about 5 and 10 prey d⁻¹, which (using average densities from the 1989 summer) is <1 prey m⁻³. With total prey densities ranging from 304 to 1380 m⁻³ (Fig. 8) this would give a removal rate <0.2% prey per day. Bollens (1988) estimated that removal rates of prey between 0.5 and 3.0% implied a significant predatory impact. We found that larvae of *Thunnus maccoyii* were able to remove up to as much as 15% of the prey population (Young and Davis 1990), which would clearly affect prey densities. In the present study, however, low numbers of larvae, together with high densities of prey species, would make a similar situation unlikely for *Trachurus declivis*. Similar studies from temperate waters have also found that larvae were too few to have an impact on their prey (Cushing 1983, Peterson and Ausubel 1984, Jenkins 1987), although Cushing (1983) pointed out that post-larvae, with their increased hunting skills, could reverse this pattern.

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CHAPTER 9

Feeding ecology and interannual variations in the diet of southern bluefin tuna (*Thunnus maccoyii*) in coastal and oceanic waters of eastern Tasmania, Australia

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Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia

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Synopsis

The diets of 1219 southern bluefin tuna, *Thunnus maccoyii*, from inshore (shelf) and offshore (oceanic) waters off eastern Tasmania were examined between 1992 and 1994. Immature fish (< 155 cm fork length) made up 88% of those examined. In all, 92 prey taxa were identified. Inshore, the main prey were fish (*Trachurus declivis* and *Emmelichthys nitidus*) and juvenile squid (*Nototodarus gouldi*). Offshore, the diversity was greater, reflecting the diversity of micronekton in these waters. Interestingly, macrozooplankton prey (e.g. *Phronima sedentaria*) were prevalent in tuna > 150 cm. The offshore tuna, when in subantarctic waters, ate relatively more squid than when in the East Australia Current. In the latter, fish and crustacea were more important, although there were variations between years. No relationship was found between either prey type or size with size of tuna. Feeding was significantly higher in the morning than at other times of the day. The mean weight of prey was significantly higher in inshore-caught tuna than in those caught offshore. We estimated that the mean daily ration of southern bluefin tuna off eastern Tasmania was 0.97% of wet body weight day⁻¹. However, the daily ration of inshore-caught tuna was ~ 3 times higher (2.7%) than for tuna caught offshore (0.8%) indicating that feeding conditions on the shelf were better than those offshore. Our results indicate that the inshore waters of eastern Tasmania are an important feeding area for, at least, immature southern bluefin tuna.

Introduction

Previous studies of the diets of tuna indicate that they are generally opportunistic feeders, eating a mixture of fish, crustacea and squid, the proportions of which depend largely on the available food supply (Serventy 1956, Shingu 1981). Southern bluefin tuna, *Thunnus maccoyii*, feed on a variety of zooplankton and micronekton species reflecting the different habitats they occupy. In coastal waters of southeastern Australia they feed on jack mackerel *Trachurus declivis*, pilchards *Sardinops neopil-*

chardus, squid *Nototodarus gouldi* and krill *Nyctiphanes australis* (Serventy 1956). Offshore, pelagic species of crustacea (e.g. *Phronima sedentaria*), squid and pelagic fish (e.g. *Brama brama*) are more common prey species (Robins 1963, Talbot & Penrith 1963, Webb 1972). The deep-sea penaeid *Funchalia woodwardi* has also been reported as prey of southern bluefin tuna south of Africa (Talbot & Penrith 1963), indicating they can feed at depth, where light is low. However, these differences have not been quantified in relation to specific water masses. There is also little information on other as-

pects of the feeding ecology of southern bluefin tuna, such as the daily ration of wild-caught southern bluefin tuna.

Southern bluefin tuna migrate annually from the Great Australian Bight to waters off eastern Tasmania where fish ranging in size from ± 50 to 190 cm are taken by the domestic troll and Japanese longline fisheries, although smaller and larger fish are occasionally taken (Caton et al.¹). The majority of fish caught are sub-adults as most are smaller than the estimated size at maturity of ~ 155 cm (Davis²).

Southern bluefin tuna have been reported to school at oceanic fronts in the south-west Tasman Sea (Robins 1952, Hynd 1968, 1969, Shingu 1981). Shingu (1981) found that the fishing effort of Japanese longliners off the east coast of Tasmania was closely associated with the temperature front separating warm East Australia Current water from cooler subantarctic water. He observed that these tuna schooled in areas 'where the isotherms lie in a tongue-like shape and . . . where the temperature gradient is great'. It is generally assumed that these tuna were aggregating in areas of greater prey availability near the front. This assumption is supported by evidence of increased nutrient and zooplankton concentrations at the edge of two separate offshore fronts in this region (Tranter et al. 1983, Young & Lyne 1993). However, as a ten-mile exclusion zone for foreign-owned longliners operates off the coast of Tasmania, the importance of the neighbouring shelf waters as feeding grounds for the tuna may have been overlooked.

The dominant feature of the waters off eastern Tasmania is the filament of East Australia Current (EAC) water that flows down the east coast of Australia and dissipates at, or south of, Tasmania (Harris et al. 1987). The boundary between the EAC and subantarctic water to the south is the subtropical convergence, which is generally near 42 °S. The southward extension of this filament varies be-

tween years, which can have a profound effect on the ecology of the coastal regions of Tasmania (Harris et al. 1991, Young & Davis 1992, Young et al. 1993, Jordan et al. 1995). Previous studies of the EAC and its tributaries have found significant differences in the productivity and species composition of these waters (e.g. Griffiths & Wadley 1986). Generally, the waters of the EAC and associated eddies are lower in nutrients and micronekton than are surrounding waters (Brandt 1981, Tranter et al. 1983). In contrast, the waters of the Tasmanian shelf are composed of a generally northward flowing, nutrient-rich subantarctic water, which supports large stocks of krill *Nyctiphanes australis* and their main predator, jack mackerel *Trachurus declivis* (Young et al. 1993). Both species are important prey items of southern bluefin tuna (Webb 1972).

The Tasmanian southern bluefin tuna fishery is recognised not only as a fishing area but also an indicator of the health of the overall fishery. With increasing pressure to lift quotas, an understanding of the factors leading to variations in catch rate, both temporal and spatial, is needed. A three-year study was therefore initiated to examine the physical and biological environment of the southern bluefin off eastern Tasmania (Young et al. 1996a). In this paper we aim to (1) describe the feeding ecology of southern bluefin in the waters of eastern Tasmania, and (2) examine annual variations in prey composition and feeding success in relation to the regional oceanography. Finally, we aim to (3) estimate the daily ration of southern bluefin tuna off eastern Tasmania.

Materials and methods

Stomachs of southern bluefin tuna were collected in 1992, 1993 and 1994 during the Tasmanian southern bluefin fishing season, which generally lasts between May and July (Shingu 1981). Stomachs were collected from two sources – the inshore troll fishery around the Hippolyte Rocks area, and from the Australian Fishing Zone observer program in oceanic waters off eastern Tasmania (Figure 1). Inshore, stomachs were removed immediately on capture and transferred to an ice slurry, and time, place

¹ Caton, A., P. Ward & C. Colgan. 1995. The Australian 1989–1990 to 1994–5 southern bluefin tuna seasons. Council for the conservation of Southern Bluefin Tuna Scientific Meeting, 10–19 July 1995.

² Davis, T.L.O. 1995. Size at first maturity of southern bluefin tuna. Council for the conservation of Southern Bluefin Tuna Scientific Meeting, 10–19 July 1995.

of capture, size (length to caudal fork [LCF] in cm) and weight of fish ($\text{kg} \pm 0.5$ wet weight) recorded. The stomachs were later frozen and transferred to the laboratory for processing. Offshore, the same procedures were followed except that the place of collection was estimated from the closest beacon to which the fish was caught.

Laboratory analyses

In the laboratory, the stomachs were opened and assigned a subjective index of fullness (1 = empty, 2 < half full, 3 = half full, 4 half full, 5 = full), and state of digestion (1 = undigested, 2 = part digested, 3 = well digested). The contents were then removed and weighed en masse (± 0.5 g). Prey items were identified to the lowest possible taxon, counted, measured along the longest axis (± 2.5 mm) and weighed (± 0.5 g). Items identified as longline bait were discarded.

Data analysis

Length frequencies of inshore and offshore-caught fish were compared using the Komolgorov-Smirnov (K-S) test. Diet composition was analysed by a modification of the weight method of Bigg & Perez (1985). The advantage of this method is that it does not overemphasise the importance of numerous small prey items (see Pinkas et al. 1971). Furthermore, by initially ranking prey items by frequency of occurrence it reduces biases caused by the different rates of digestion of various prey taxa, and eliminates the effect of trace remains by using only fleshy remains as evidence of diet.

Prey taxa were grouped into fish, cephalopods, crustaceans and gelatinous zooplankton. The proportions of these groups in the diet were determined by frequency of occurrence, corrected to 100%. The proportion of an individual taxon within each major group was then determined by weight. Trace remains; squid beaks, otoliths and fish bones were ignored (see Bigg & Perez 1985). The 'barrels', manufactured by some species of amphipods from salps or siphonophores, were also ignored. Barrels

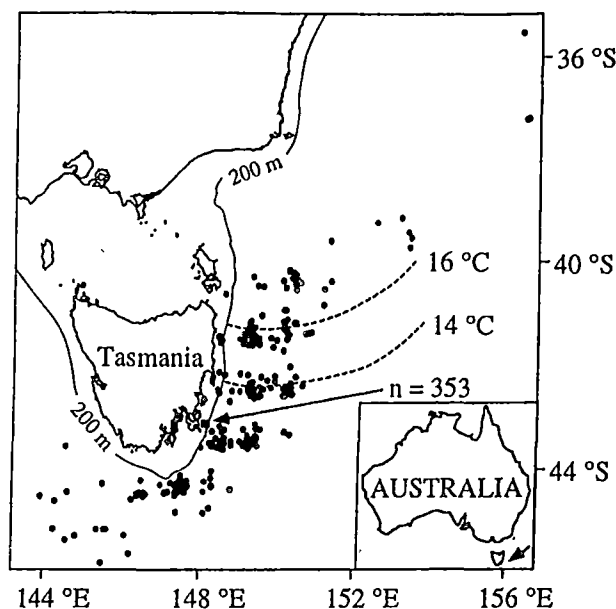


Figure 1. Study areas showing capture positions of southern bluefin tuna off eastern Tasmania, Australia, between 1992 and 1994. Surface isotherms are diagrammatic (n = number of stomachs from inshore waters).

appear to remain in the stomach considerably longer than the crustaceans they originally housed and are believed to contribute very little to the diet of fish. Those made from the tunica of salps are probably not assimilated because of their mucopolysaccharide content (Kashkina 1986), and those constructed from siphonophores have a similar chemical structure and very low nutritional value (Clarke et al. 1992).

The stomachs from tuna caught offshore were categorised, through satellite imagery, into three groups based on sea surface temperature: warm (East Australia Current; $T > 16^\circ\text{C}$), intermediate (Subtropical Convergence; $14 \leq T \leq 16^\circ\text{C}$) or cool (Subantarctic water; $T \leq 14^\circ\text{C}$) for each of the three years. A full description of these water masses during the study period is given in Young et al. (1996a).

Diet overlap was compared between areas (inshore and the three offshore areas) and size groupings (20 cm length intervals) for the three years, using the Spearman rank correlation coefficient, r_s (Zar 1984). Prey taxa were ranked by modified weight for the comparison. Values of r_s range between -1 (perfect negative correlation) and $+1$ (perfect correlation). The test for significance com-

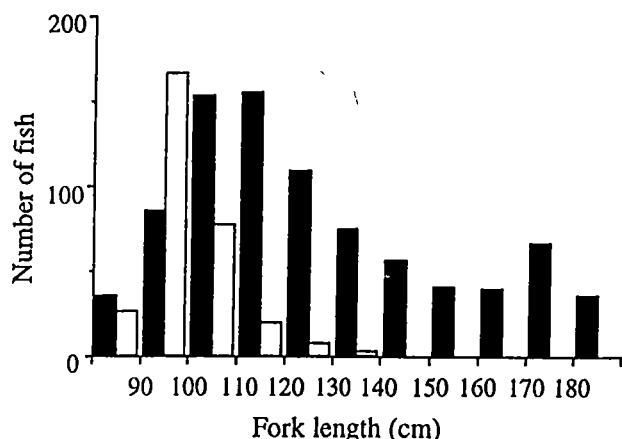


Figure 2. Length-frequency distributions of southern bluefin tuna caught in inshore (open bars) and offshore (closed bars) waters of eastern Tasmania, Australia.

compares the value to 0, so a result that is significantly different from zero indicates an overlap in the diets of the pair being tested. Diet breadth was measured by Levin's index, $B = (\sum p_i^2)^{-1}$, where p_i = proportion of a prey taxon in the diet, standardised to fractions (after Hespeneheide 1975).

Food consumption over hourly interval ($C_{\Delta t}$ g $\text{kg}^{-1} \cdot \text{h}^{-1}$) was calculated (following Elliot & Persson 1978 and Boisclair & Marchand 1993) by the equation:

$$C_{\Delta t} = \frac{(F_{t+1} - F_t e^{-RT})}{(1 - e^{-RT})}, \quad (1)$$

where F_t and F_{t+1} are the geometric means of the ratio of stomach contents (g wet weight) to whole weight of predator (kg wet weight) at the beginning and end of each one hour period, T = time period and R is the exponential rate of gastric evacuation. Gastric evacuation rate (R , h^{-1}) was estimated (following Boisclair & Marchand 1993) as the maxi-

mum rate at which food was evacuated during any one hour period,

$$R = \frac{\ln F_{t+1} - \ln F_t}{2}. \quad (2)$$

This method of estimating gastric evacuation rate assumes that no feeding occurs during the period of greatest rate of food evacuation. In a species that feeds continuously, this method will underestimate the rate of gastric evacuation. However, it offers the advantage that it can be used on field data, without using captive experimental animals.

Neither the inshore nor offshore fleets fished continuously for 24 h. We therefore gave values of food consumption initially for only the time period sampled, and then extended this result to a full 24 h period, using the formula

$$D = \left(\sum_{i=1}^p C_{\Delta t_i} \right) \frac{24}{p}, \quad (3)$$

where p is the number of time periods in which sampling was carried out. Daily ration was estimated for all size classes and areas combined. We then made separate estimates for both the inshore and offshore areas because of the wide discrepancy between rations from the two areas. Finally we compared the daily rations of small (< 140 cm LCF) and large (> 140 cm LCF) tuna from offshore waters to investigate whether the observed difference in daily ration between inshore and offshore fishes was related to size rather than position of capture. In light of the uncertainty in the elapsed time between capture and landing of longline-caught fish, we assumed that the fish were hooked shortly before death and that digestion had not progressed significantly.

Table 1. Number of southern bluefin tuna stomach samples examined from eastern and southern Tasmania, Australia, grouped according to area and year of capture.

Area of capture	1992	1993	1994	Total
Inshore	169	45	136	350
Warm	87	141	48	276
Intermediate	115	126	63	304
Cool	21	66	184	271
Total	392	378	431	1219*

* Includes 15 samples lacking location data, collected offshore

Table 2. Food items in the stomachs of southern bluefin tuna collected from inshore and offshore waters off eastern Tasmania. % n = percentage of all stomachs which contained prey; % wt. = percentage of total weight; % f = percentage frequency of occurrence; n = number of fish examined; % n_f = percentage of fish stomachs examined containing prey. Percentage totals for each main prey item are given in parentheses; – = prey absent.

Prey	Inshore 40–130 cm LCF n = 353 % n _f = 87.3			Offshore 74–192 cm n = 870 % n _f = 86.9		
Crustacea	(27.9)	(0.2)	(8.4)	(61.0)	(1.6)	(49.3)
Copepoda	(< 0.1)	(< 0.1)	(0.3)	(–)	(–)	(–)
Unidentified Copepoda	< 0.1	< 0.1	0.3	–	–	–
Mysidacea	(–)	(–)	(–)	(< 0.1)	(< 0.1)	(0.5)
<i>Gnathopausia ingens</i>	–	–	–	< 0.1	< 0.1	0.5
Euphausiacea	(9.8)	(< 0.1)	(0.3)	(10.4)	(< 0.1)	(6.7)
<i>Euphausia spinifera</i>	–	–	–	1.1	< 0.1	0.1
<i>Nyctiphanes australis</i>	9.8	< 0.1	0.3	–	–	–
Unidentified Euphausiacea	–	–	–	9.4	< 0.1	6.6
Amphipoda	(16.6)	(0.1)	(4.5)	(41.8)	(1.3)	(43.1)
<i>Brachyscelus cruscum</i>	–	–	–	3.6	< 0.1	9.1
<i>Eupronoe armata</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Parathemisto guardichardi</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Phronima sedentaria</i>	6.3	< 0.1	2.9	35.0	1.2	36.4
<i>Phrosina semilunata</i>	–	–	–	1.3	< 0.1	5.7
<i>Platyscelus ovoides</i>	–	–	–	1.1	< 0.1	4.9
<i>Pronoe capito</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Streetsia challengerii</i>	< 0.1	< 0.1	0.3	–	–	–
Unidentified Amphipoda	10.2	< 0.1	1.3	0.8	< 0.1	2.0
Isopoda	(0.1)	(< 0.1)	(1.0)	(–)	(–)	(–)
Unidentified Isopoda	0.1	< 0.1	1.0	–	–	–
Decapoda	(0.4)	(< 0.1)	(1.6)	(8.7)	(0.2)	(11.9)
<i>Acantheephyra quadrispinosa</i>	–	–	–	< 0.1	< 0.1	0.1
crab megalopa	0.4	< 0.1	1.3	8.6	0.2	10.4
<i>Funchalia</i> spp.	–	–	–	< 0.1	< 0.1	0.1
<i>Gennadas</i> spp.	–	–	–	< 0.1	< 0.1	0.3
<i>Sergestes arcticus</i>	–	–	–	< 0.1	< 0.1	0.3
Unidentified Caridae	–	–	–	< 0.1	< 0.1	0.7
Unidentified Penaeidae	< 0.1	< 0.1	0.3	< 0.1	< 0.1	0.1
Unidentified Decapoda	–	–	–	< 0.1	< 0.1	0.1
Stomatopoda	(0.8)	(< 0.1)	(3.2)	(< 0.1)	(< 0.1)	(0.1)
Unidentified Stomatopoda	0.8	< 0.1	3.2	< 0.1	< 0.1	0.1
Unidentified Crustacea	< 0.1	< 0.1	0.3	< 0.1	< 0.1	1.1
Annelida	(0.1)	(< 0.1)	(0.6)	(–)	(–)	(–)
Unidentified Polychaetae	0.1	< 0.1	0.6	–	–	–
Mollusca	(11.6)	(14.0)	(24.4)	(18.5)	(54.0)	(63.2)
Gastropoda	(–)	(–)	(–)	(< 0.1)	(< 0.1)	(0.1)
Unidentified Gastropoda	–	–	–	< 0.1	< 0.1	0.1
Pteropoda	(–)	(–)	(–)	(0.2)	(< 0.1)	(1.6)
<i>Cavolinia uncinata</i>	–	–	–	< 0.1	< 0.1	0.3
<i>Diacria trispinosa</i>	–	–	–	< 0.1	< 0.1	0.4
Unidentified Pteropoda	–	–	–	0.1	< 0.1	0.9
Cephalopoda	(13.8)	(14.1)	(30.2)	(21.3)	(54.1)	(69.3)
<i>Argonauta nodosa</i>	0.3	0.4	1.9	1.9	6.0	16.4
<i>Enoploteuthis galaxias</i>	–	–	–	< 0.1	< 0.1	0.3

Table 2. Continued.

Prey	Inshore 40–130 cm LCF n = 353 % n _t = 87.3			Offshore 74–192 cm n = 870 % n _t = 86.9		
<i>Histioteuthis</i> spp.	–	–	–	0.3	0.3	4.2
<i>Lepidoteuthis</i> spp.	–	–	–	< 0.1	< 0.1	0.5
<i>Lycoteuthis lorigera</i>	–	–	–	7.3	7.1	14.3
<i>Nototodarus gouldi</i>	6.7	10.6	7.5	4.8	25.2	18.1
<i>Ochytioe tuberculata</i>	–	–	–	0.3	1.4	3.7
<i>Sepioteuthis australis</i>	–	–	–	< 0.1	0.3	0.1
<i>Teuthowenia pellucida</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Todarodes filipovae</i>	–	–	–	0.3	2.7	3.8
<i>Tremoctopus violaceus</i>	–	–	–	< 0.1	< 0.1	0.1
Cephalopod larvae	–	–	–	0.3	< 0.1	0.8
Unidentified Octopoda	0.6	0.2	0.3	0.3	0.3	3.3
Unidentified Ommastrephidae	0.4	0.1	0.6	0.8	4.3	5.3
Unidentified Onychoteuthidae	–	–	–	< 0.1	0.3	1.1
Unidentified Cephalopoda	3.5	2.7	14.3	1.8	6.1	14.7
Cephalopod beaks	2.3	< 0.1	6.5	3.0	< 0.1	11.1
Unidentified Mollusca	–	–	–	0.1	< 0.1	0.1
Tunicata	(1.6)	(< 0.1)	(1.9)	(6.7)	(1.1)	(9.4)
Thaliacea	(1.1)	(< 0.1)	(1.3)	(2.2)	(0.1)	(6.1)
Unidentified Thaliacea	1.1	< 0.1	1.3	2.2	0.1	6.1
Pyrosomatidae	(0.5)	(< 0.1)	(1.3)	(4.5)	(0.9)	(3.6)
<i>Pyrosomas atlanticum</i>	0.5	< 0.1	1.3	4.5	0.9	3.6
Pisces	(63.1)	(86.0)	(89.9)	(12.4)	(43.2)	(57.3)
Clupeiformes	(3.1)	(0.5)	(2.6)	(0.1)	(1.0)	(1.7)
<i>Engraulis australis</i>	3.1	0.5	2.6	–	–	–
<i>Sardinops neopilchardus</i>	–	–	–	0.1	1.0	1.7
Gonorynchiformes	(–)	(–) (–)	(0.7)	(< 0.1)	(0.1)	
<i>Gonorynchus greyi</i>	–	–	–	0.7	< 0.1	0.1
Stomiiformes	(–)	(–)	(–)	(< 0.1)	(< 0.1)	(0.5)
<i>Photichthys argenteus</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Sternoptyx</i> spp.	–	–	–	< 0.1	< 0.1	0.4
Aulopiformes	(–)	(–)	(–)	(1.6)	(0.6)	(1.5)
<i>Scopelosaurus</i> spp.	–	–	–	< 0.1	0.5	0.9
Unidentified Paralepididae	–	–	–	1.5	0.2	0.7
Myctophiformes	(3.8)	(0.7)	(1.0)	(0.6)	(0.3)	(0.8)
<i>Lampanyctus</i> spp.	–	–	–	< 0.1	< 0.1	0.3
<i>Symbolophorous barnardi</i>	–	–	–	< 0.1	< 0.1	0.1
Unidentified Myctophidae	3.8	0.7	1.0	0.6	0.3	0.4
Beloniformes	(2.5)	(0.5)	(2.9)	(1.5)	(< 0.1)	(0.4)
<i>Hyporhamphus melanochir</i>	2.4	0.4	1.9	–	–	–
<i>Scomberesox forsteri</i>	0.1	< 0.1	1.0	–	–	–
Unidentified Hemiramphidae	–	–	–	1.5	< 0.1	0.4
Beryciformes	(–)	(–)	(–)	(< 0.1)	(< 0.1)	(0.1)
<i>Diretmus argenteus</i>	–	–	–	< 0.1	< 0.1	0.1
Zeiiformes	(–)	(–)	(–)	(< 0.1)	(< 0.1)	(0.1)
<i>Oreosoma atlanticum</i>	–	–	–	< 0.1	< 0.1	0.1
Syngnathiformes	(0.2)	(< 0.1)	(0.6)	(0.1)	(< 0.1)	(1.7)
<i>Hippocampus</i> spp.	0.1	< 0.1	0.3	< 0.1	< 0.1	1.5
<i>Macroramphosus scolopax</i>	< 0.1	< 0.1	0.3	< 0.1	< 0.1	0.3

Table 2. Continued.

Prey	Inshore 40–130 cm LCF n = 353 % n _t = 87.3			Offshore 74–192 cm n = 870 % n _t = 86.9		
Unidentified Syngnathidae	–	–	–	–	–	–
Perciformes	(34.4)	(82.4)	(67.9)	(2.7)	(39.0)	(31.6)
<i>Anthias pulchellus</i>	0.4	0.9	2.9	< 0.1	< 0.1	0.1
<i>Brama brama</i>	–	–	–	0.1	8.7	2.6
<i>Cubiceps baxteri</i>	–	–	–	< 0.1	0.7	0.9
<i>Cubiceps caeruleus</i>	–	–	–	0.1	1.2	1.6
<i>Emmelichthys nitidus</i>	17.0	30.5	31.2	0.2	1.4	1.5
<i>Gasterochisma melampus</i>	0.1	0.5	0.6	–	–	–
<i>Plagiogenion rubiginosus</i>	< 0.1	< 0.1	0.3	–	–	–
<i>Pseudopentaceros richardsoni</i>	–	–	–	< 0.1	0.8	0.3
<i>Pteraclis velifera</i>	–	–	–	< 0.1	0.1	0.4
<i>Tetragonurus cuvieri</i>	–	–	–	< 0.1	0.1	0.1
<i>Thyrsites atun</i>	2.5	4.4	5.2	0.2	1.2	3.2
<i>Trachurus declivis</i>	14.3	45.8	43.8	1.9	24.5	22.6
Unidentified Gempylidae	–	–	–	< 0.1	< 0.1	0.1
Unidentified Pentacerotidae	–	–	–	< 0.1	< 0.1	0.3
unidentified Serranidae	< 0.1	< 0.1	0.3	–	–	–
Tetraodontiformes	(–)	(–)	(–)	(< 0.1)	(0.3)	(1.1)
<i>Lactoria diaphana</i>	–	–	–	< 0.1	< 0.1	0.1
<i>Lagocephalus</i> spp.	–	–	–	< 0.1	< 0.1	0.3
Unidentified Monacanthidae	–	–	–	< 0.1	< 0.1	0.1
Fish bones	2.8	0.3	8.8	0.3	< 0.1	3.8
Fish scales	0.1	< 0.1	1.0	–	–	–
Otoliths	3.8	< 0.1	1.0	1.5	< 0.1	2.1
Unidentified pisces	5.4	1.2	18.2	1.4	1.6	18.7
Unidentified remains	< 0.1	< 0.1	0.3	< 0.1	< 0.1	0.3
Macroalgae	0.2	< 0.1	< 1.6	0.1	< 0.1	2.5
Marine pollution	–	–	–	–	–	1.6
Total number and weight	2041	58205.7 g	–	13454	133445.2 g	–

Results

The stomach contents of 1219 southern bluefin tuna captured during the winters of 1992, 1993 and 1994 were examined (Table 1). Tuna captured inshore ranged in size from 40 to 130 cm (2.5–60.0 kg) and were significantly smaller than those tuna caught offshore ($K-S$, $D_{\max} = 58.03$, $D_{0.05} = 10.96$, $n_1 = 299$, $n_2 = 846$, $P < 0.05$). The latter ranged in size from 74 to 192 cm (15.0–145.0 kg) (Figure 2). Following Davis² only 12% were mature, and these were all collected from offshore waters.

Composition of diet

In all, 92 prey taxa were identified – 36 species of fish, 16 of squid, 25 of crustacea and the remainder of molluscs, annelids, tunicates and algae (Table 2). Prey ranged in size from small crustacea (e.g. *Brachyscelus cruscolum*) < 1 cm in length and 0.1 g in weight to fish over 50 cm and 4 kg (e.g. *Brama brama*).

There were some marked differences between the diets of tuna from inshore and offshore waters. First, prey diversity was much lower inshore (38 prey taxa) than offshore (78 prey taxa) (Table 2). Second, the type and relative amount of prey taxa differed between the two main areas.

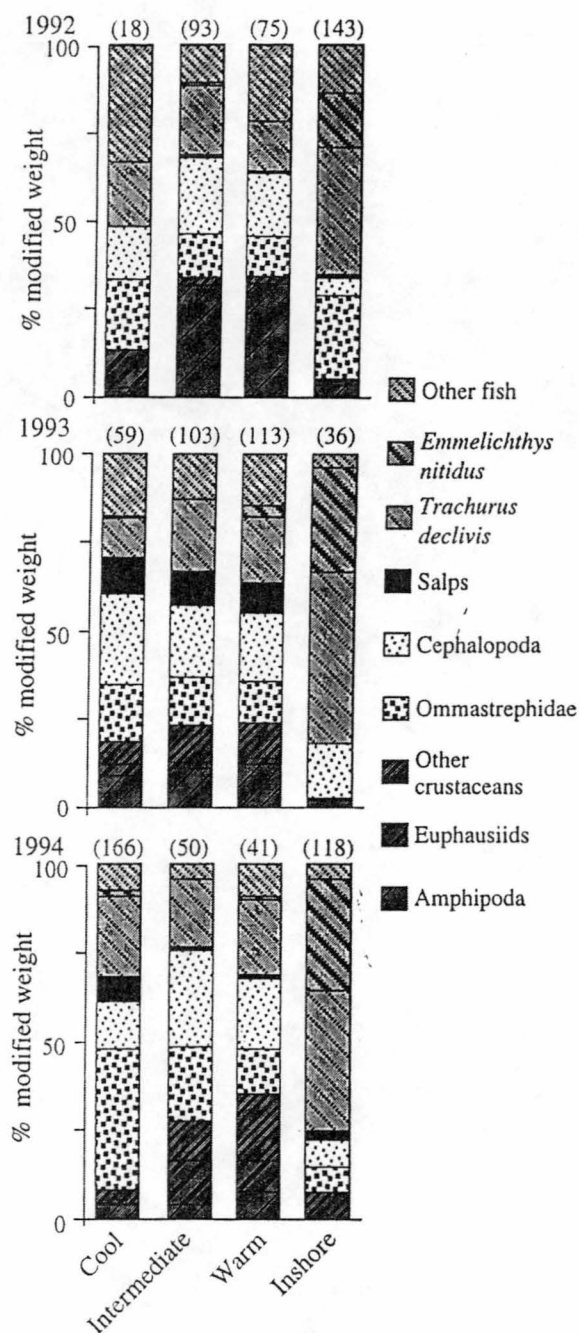


Figure 3. Relative proportions of the main prey taxa of southern bluefin tuna in the main water masses and inshore waters of eastern Tasmania, Australia, between 1992 and 1994.

Inshore, fish were the main prey, mainly due to two species, jack mackerel *Trachurus declivis* and redbait *Emmelichthys nitidus*. Although crustaceans were next in order of frequency of occurrence, they contributed little in terms of biomass. Pelagic amphipods, not normally found over the

shelf, were unexpectedly frequent. Tuna from the shelf with stomachs full of krill *Nyctiphanes australis* were reported to one of us (JWY) by local fishers, but few of these samples were kept. Cephalopods – mainly of juvenile *Nototodarus gouldi* (mantle length $49.05 \text{ mm} \pm 1.35 \text{ SE}$), were the second most important prey taxon in inshore-caught tuna. Offshore, Crustacea (mainly *Phronima sedentaria*) were the most common prey taxon by frequency of occurrence, but contributed little to overall biomass. A diverse mix of cephalopod species, but mainly *Lycoteuthis lorigera* and adult *Nototodarus gouldi* (mantle length $85.78 \text{ mm} \pm 2.56 \text{ SE}$), made up the largest component of the diet offshore. Next in importance was a variety of fish species. That the largest component of this group was jack mackerel, normally associated with shelf and shelf break waters, highlights the exchange of fish between inshore and offshore waters.

The relative proportions of the nine main taxa differed most between the inshore and offshore samples (Figure 3). Offshore, these differences were relatively small. In the offshore diet overlap comparisons, approximately half significantly overlapped over the three-year period. In contrast, only one overlap was significant in the inshore comparisons – between 1993 and 1994 inshore samples (Table 3). Such a large number of pairings for which there was no significant overlap indicates marked changes in the relative abundance of particular prey taxa. For example, salps were not present in offshore samples in 1992, but were present in 1993 and in 1994. Plankton sampling and midwater trawling over the three-year period showed a similar pattern (Young et al. 1996a,b). Amphipods were progressively less important over the three years, whereas other crustaceans – mainly crab megalopa – increased in importance. There were no overlaps between 1992 and 1994, in any area. Two patterns that also emerged were that cephalopods became more common, and crustaceans less common, in tuna stomachs as the sea surface temperature decreased (Figure 3).

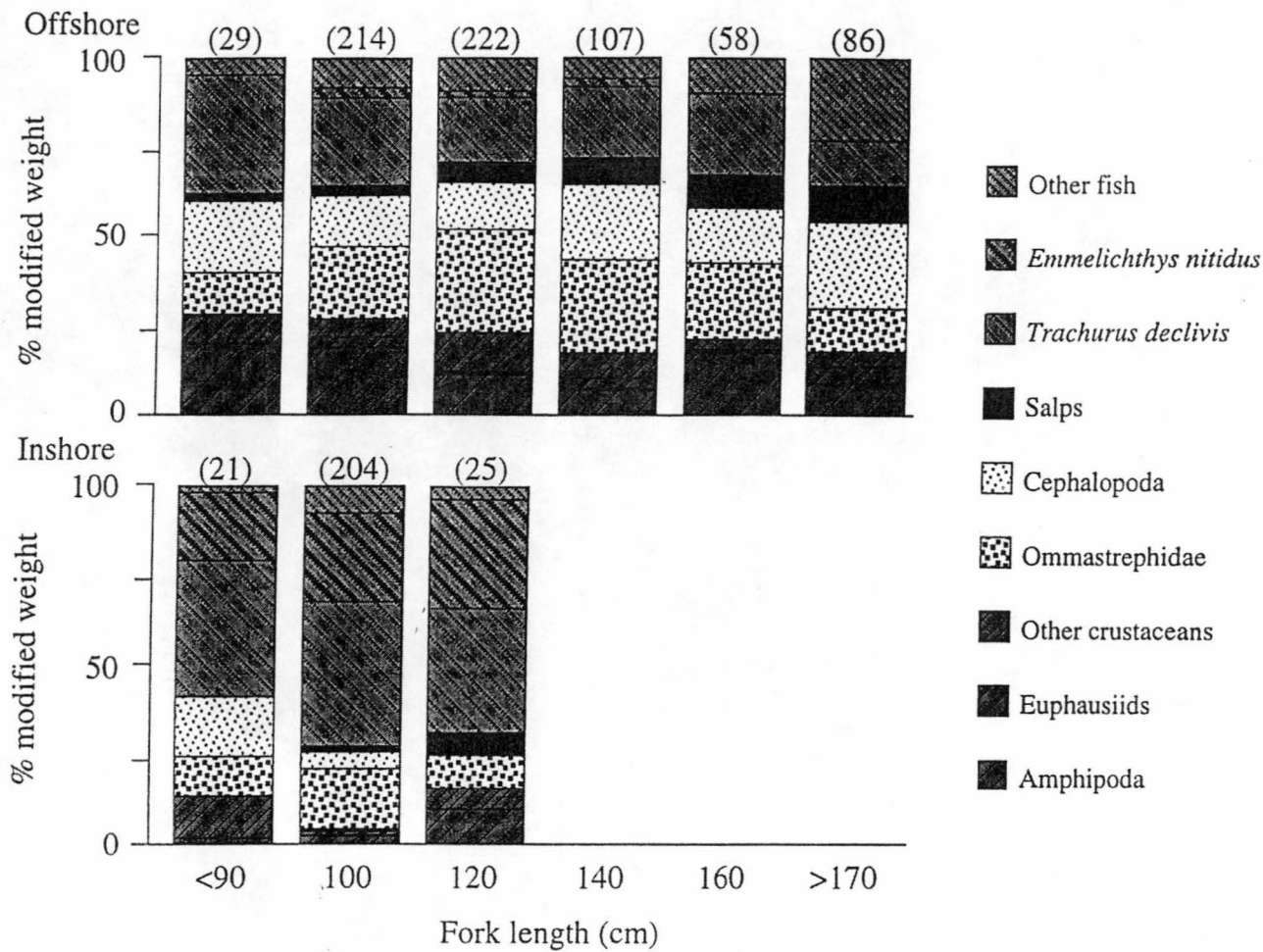


Figure 4. Relative proportions of the main prey taxa of southern bluefin tuna in relation to size of tuna from inshore and offshore waters of eastern Tasmania, Australia.

Table 3. Diet overlap, using the Spearman rank correlation, ρ_s , between southern bluefin tuna collected from each area off eastern Tasmania, Australia, for each of the three years. Underlined values are significantly correlated at $p \leq 0.05$.

		Cool		Intermediate			Warm			Inshore		
		1993	1994	1992	1993	1994	1992	1993	1994	1992	1993	1994
Cool	1992	<u>0.729</u>	0.678	0.407	<u>0.695</u>	0.610	0.559	0.593	0.525	0.627	0.241	0.051
	1993		<u>0.850</u>	0.567	<u>0.883</u>	0.600	0.683	<u>0.833</u>	0.583	0.333	0.220	0.167
	1994			0.600	<u>0.867</u>	0.583	0.533	<u>0.750</u>	0.600	0.600	0.322	0.383
Intermediate	1992				<u>0.783</u>	0.400	<u>0.850</u>	<u>0.850</u>	0.483	0.400	0.271	0.283
	1993					<u>0.767</u>	<u>0.733</u>	<u>0.933</u>	<u>0.817</u>	0.450	0.373	0.367
	1994						0.300	0.533	<u>0.850</u>	0.283	0.203	0.217
Warm	1992							<u>0.833</u>	0.417	0.183	0.034	-0.067
	1993								<u>0.700</u>	0.417	0.475	0.417
	1994									0.267	0.467	0.467
Inshore	1992										0.644	0.567
	1993											<u>0.932</u>

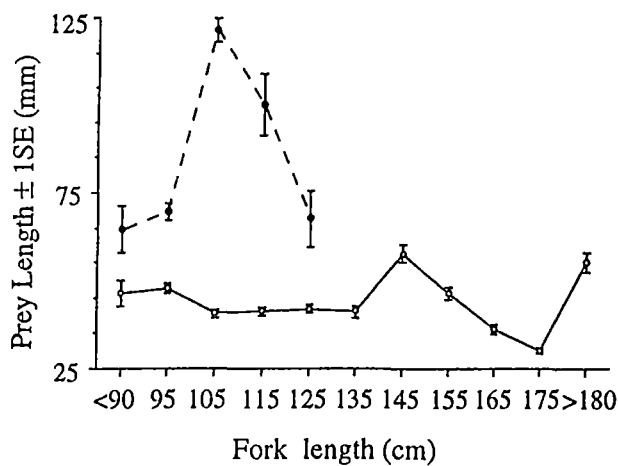


Figure 5. Relationship between prey length and size of southern bluefin tuna from inshore (dashed line) and offshore (solid line) waters of eastern Tasmania, Australia.

Relationships between tuna and their prey

As the main pattern to emerge was the difference between inshore and offshore samples, we examined a number of relationships between the tuna and their prey separately for these two regions. Offshore, prey type varied little across the size groups (Figure 4). This similarity in prey across size groupings was reflected in the significant overlaps found between length groups (Table 4). However, there were no overlaps between the diet of fish > 170 cm and smaller fish, largely due to the relatively high proportion of 'other fish'. Inshore, prey types were similar across size groupings. However, the relative proportions differed enough that prey overlap comparisons between size groups were not significant

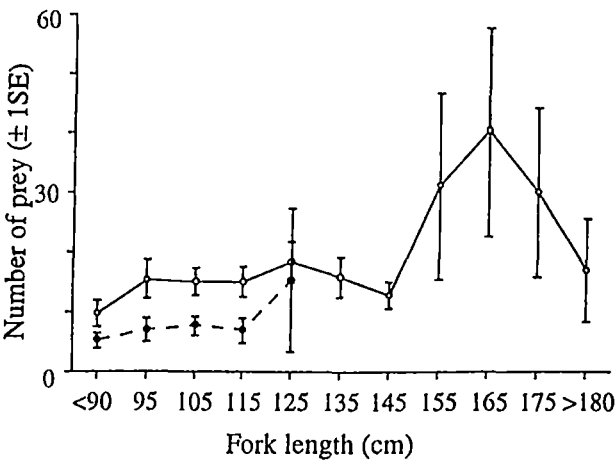


Figure 6. Relationship between numbers of prey and size of southern bluefin tuna from inshore (dashed line) and offshore (solid line) waters of eastern Tasmania, Australia.

(Table 4). For example, tuna < 90 cm ate a greater proportion of juvenile *Nototodarus gouldi* than did larger fish, whereas larger fish ate a greater proportion of fish taxa.

There was no relationship between the length of southern bluefin tuna and the length of their prey (Figure 5), or the numbers of prey (Figure 6). However, the prey of offshore fish were significantly smaller (ANOVA, $n = 860$, $df = 1$, $F = 852.69$, $p = 0.00$) and more numerous (ANOVA, $n = 914$, $df = 1$, $F = 18.92$, $p = 0.00$) than those of similarly-sized inshore fish. These differences reflected the greater importance of zooplankton in the diet of offshore fish, and of fish in the inshore tuna. Hence, gut content weight, expressed as a percentage of whole weight, was significantly higher (ANOVA, $n = 914$,

Table 4 Diet overlap, using the Spearman rank correlation, ρ_s , of different size classes of southern bluefin tuna caught in inshore and offshore waters east of Tasmania, Australia. Underlined values are significantly correlated at $p \leq 0.05$

		inshore		offshore				
		90-109	110-129	< 90	90-109	110-129	130-149	150-169
inshore	< 90	0.628	0.525	0.184	0.343	0.485	0.201	0.268
	90-109		0.628	0.300	0.417	0.417	0.217	0.450
	110-129			0.151	0.138	0.301	0.084	0.335
offshore	< 90				<u>0.833</u>	0.667	0.617	<u>0.850</u>
	90-109					<u>0.933</u>	<u>0.783</u>	<u>0.983</u>
	110-129						<u>0.867</u>	<u>0.900</u>
	130-149							<u>0.817</u>
	150-169							

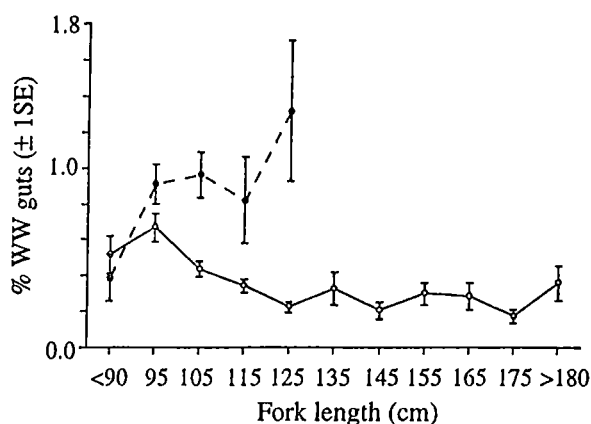


Figure 7. Relationship between % WW Guts and size of southern bluefin tuna from inshore and offshore waters of eastern Tasmania (% WW guts: ratio [%] of wet weight of stomach contents to total fish wet weight).

$df = 1$, $F = 28.45$, $p = 0.00$) in inshore fish than in fish of the same size from offshore (Figure 7).

Gut content weight was not significantly different between years among the inshore fish (Figure 8a) (ANOVA, $n = 146$, $df = 2$, $F = 1.64$, $p = 0.20$). However, there was a significant decline in gut content weight in offshore fish over the study period (ANOVA, $n = 631$, $df = 2$, $F = 3.62$, $p = 0.03$). The mean number of prey in the guts of both offshore fish and inshore fish were not significantly different over the three years (Figure 8b) (ANOVA, $n = 714$, $df = 2$, $F = 2.21$, $p = 0.11$ and $n = 282$, $df = 2$, $F = 0.31$, $p = 0.73$, respectively). The contrast between the mean number of prey and mean percentage weight of gut contents of the inshore and offshore fish underlined the differences in prey composition outlined earlier.

Diet breadth

Diet breadths were generally similar in tuna from the inshore and three offshore areas, with only minor fluctuations between years (Figure 9). Similarly, no consistent trend with LCF was apparent (Figure 10).

Diel changes in feeding

Overall, there was a significant difference in feed-

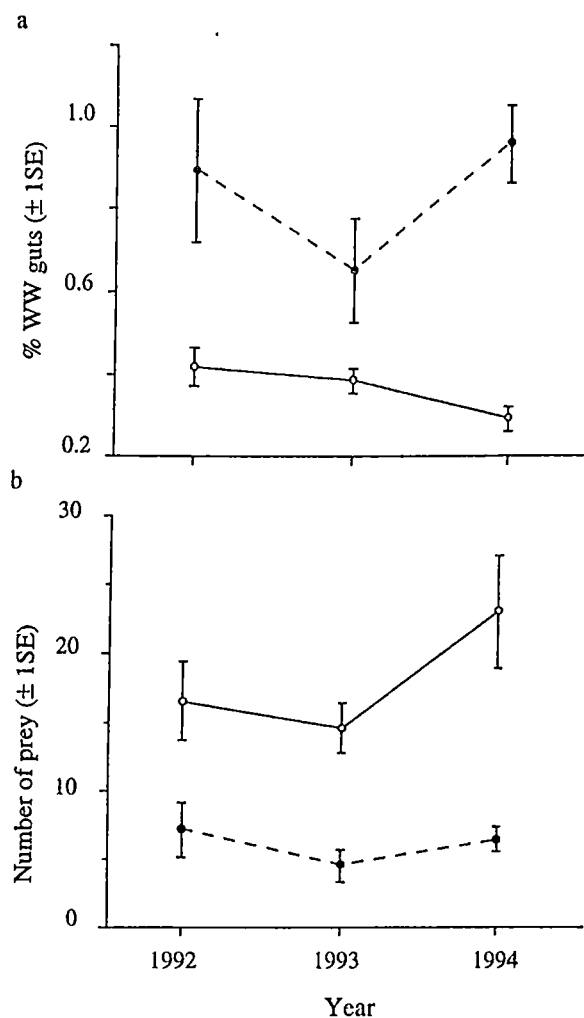


Figure 8. Interannual variations in (a) % WW guts and (b) number of prey from inshore- (dashed line) and offshore-caught (solid line) southern bluefin tuna from eastern Tasmania, Australia. % WW guts (see Figure 7).

ing with respect to time of day (ANOVA, $df = 16$, $F = 1.85$, $p = 0.02$). Feeding peaked in the early morning and declined through the day (Figure 11). However, that relationship was derived from the combination of inshore and offshore data sets. When examined separately, feeding did not vary significantly with respect to time of day for either the inshore-caught (ANOVA, $n = 109$, $df = 7$, $F = 0.30$, $p = 0.95$) or offshore-caught (ANOVA, $n = 957$, $df = 14$, $F = 0.68$, $p = 0.80$) tuna. It should be noted, however, that we had no offshore data from the time when feeding was at its highest inshore. We examined daily feeding patterns further through the indirect measure of state of digestion, but found

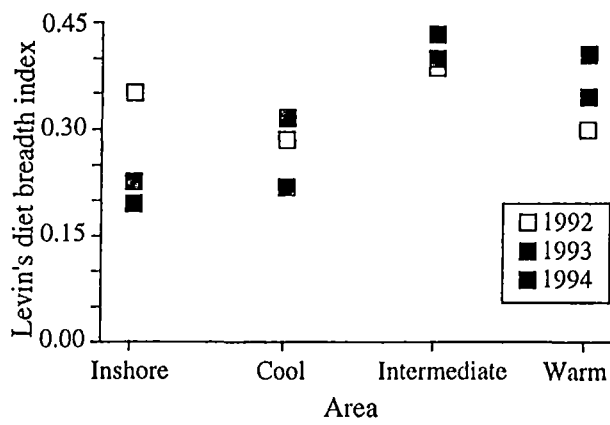


Figure 9. Interannual variations in diet breadth of southern bluefin tuna in relation to area of capture off eastern Tasmania, Australia.

no significant difference with time of day (ANOVA, $df = 20$, $F = 1.51$, $p = 0.13$), although there was a trend of fresher (part digested) material in the tuna stomachs mid-morning and again at midnight (Figure 11b).

Daily ration

From the combination of inshore and offshore data, we found that southern bluefin tuna off eastern Tasmania ate 7.28 g (prey wet wt) kg^{-1} (body wet wt) over the sampling period of 21 hours, or, using an instantaneous rate of gastric evacuation (R) of $-0.32 h^{-1}$, 0.97% of body weight per day. Taken separately, inshore fish ate 8.99 g (prey wet wt) kg^{-1} (body wet wt) in the 8-hour sampling period, or 2.69% of body weight per day ($BW d^{-1}$) ($R = -0.42 h^{-1}$). Fish captured offshore ate 6.74 g kg^{-1} in the 17-hour sampling period, or 0.81% $BW d^{-1}$ ($R = -0.32 h^{-1}$). There was little difference in the daily rations of small (<140 cm LCF; 1.01% $BW d^{-1}$) and large (≥ 140 cm LCF; 0.89% $BW d^{-1}$) southern bluefin tuna captured offshore, indicating that the difference in ration between inshore and offshore was not size-based. Offshore, there was no difference in daily ration between tuna caught in cool (1.19% $BW d^{-1}$) or warm (1.21% $BW d^{-1}$) waters. However, the daily ration of fish caught in STC water was lower (0.73% $BW d^{-1}$).

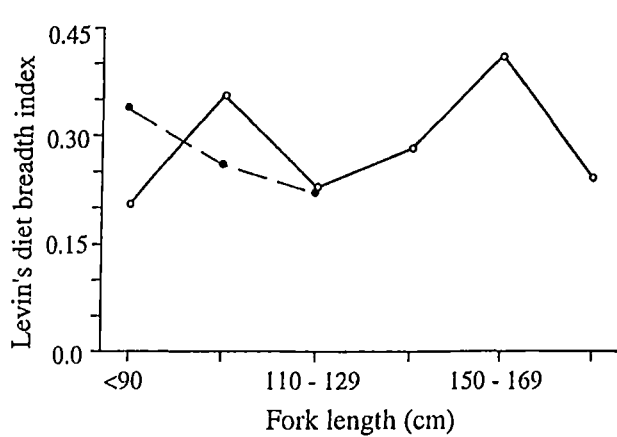


Figure 10. Relationship between diet breadth and size of southern bluefin tuna from inshore (dashed line) and offshore (solid line) waters of eastern Tasmania, Australia.

Marine pollution

Twelve southern bluefin tuna, representing 1.4% of the fish collected offshore, contained foreign material in their stomachs: plastic bags and packaging, waste from fishing operations (including rope and line) and organic galley waste. No foreign matter was found in the stomachs of fish caught in the inshore region.

Discussion

The diet of southern bluefin tuna consisted of a wide variety of prey taxa over a wide size range. In the inshore region, fish (*Trachurus declivis* and *Emmelichthys nitidus*) and juvenile squid *Nototodarus gouldi* were the main prey. Offshore, there was a greater diversity, with more macrozooplankton prey (notably *Phronima sedentaria*) than in inshore waters.

In southern and eastern Australian coastal waters, southern bluefin tuna preyed predominantly on jack mackerel *Trachurus declivis*, and pilchards *Sardinops neopilchardus*; *Nototodarus gouldi* was the most commonly eaten cephalopod, and *Nyctiphanes australis* the predominant crustacean (Serventy 1956). Southern bluefin tuna caught on longlines off northern New Zealand had eaten a variety of pelagic fish species, crustaceans (including amphipods, euphausiids and penaeids), as well as

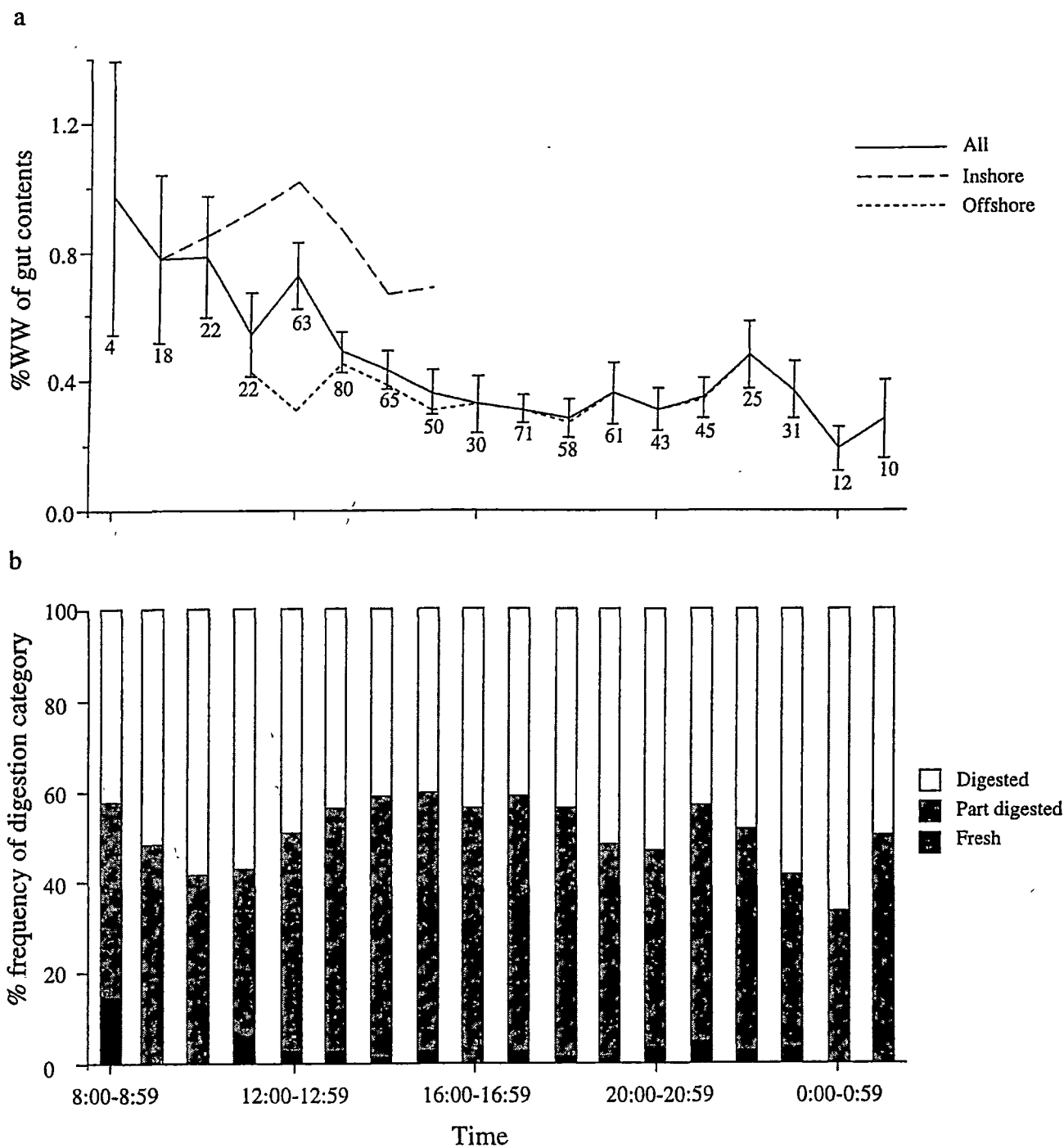


Figure 11. a – Stomach fullness (% WW guts) and b – digestion interval in relation to time of day for southern bluefin tuna caught off eastern Tasmania, Australia

squid and octopus (Robins 1963). Nine southern bluefin, caught on longlines off the coast of south west New Zealand, contained Ray's bream *Brama brama* and salps (Webb 1972). In another study, from further offshore, cephalopods were of minor

importance, whereas *Phronima sedentaria* was found in a large number of individuals (Talbot & Penrith 1963). It is surprising that the latter species, which would appear to have little nutritional value, appears so regularly in the diet of southern bluefin

tuna. The general finding of all these studies is that southern bluefin tuna will take advantage of the most readily available pelagic prey in an area. They tend to rely heavily on abundant shoaling fish species, although in the absence of such a resource, these tuna will exploit cephalopod and crustacean stocks.

We found distinct differences in diet between inshore- and offshore-caught tuna. Inshore fish ate more food than offshore fish, and different types of prey were important in their diet. These differences appear to be related to the regional oceanography. In a parallel study we found that the shelf off eastern Tasmania had a consistently higher biomass of zooplankton and micronekton than offshore waters, including the waters of the main front off eastern Tasmania (Young et al. 1996a). The reasons for the comparatively higher production in the inshore region are discussed further in that paper, but in summary, appear to result from the mixing of the inner edge of the south-flowing East Australia Current with the Zeehan Current and nutrient-rich subantarctic water.

We suggest that the migration of southern bluefin tuna through Tasmanian waters is timed to coincide with autumn blooms of phytoplankton in the area (Harris et al. 1987). These blooms provide food for large stocks of krill *Nyctiphanes australis*, which are most abundant at this time (Young et al. 1993). Krill is the main prey species of jack mackerel, which move onto the shelf and form large feeding schools in late summer and autumn (Williams & Pullen 1993, Jordan et al. 1995). They, in turn, provide food for the tuna. The presence of fish such as jack mackerel in the inshore region may explain the relatively low importance of euphausiids in the diet, despite their abundance. During winter a decrease in krill biomass appears to cause a simultaneous decrease in jack mackerel as catches drop and the schools disperse (Williams & Pullen 1993, Young et al. 1993, Jordan et al. 1995). At about this time, landings from the inshore fishery for southern bluefin tuna decline, and the offshore season begins. It seems that, as the stocks of schooling jack mackerel and redbait disperse and move into deeper water, the southern bluefin tuna leave the inshore region and move further afield in search of prey.

The low abundance of shoaling fish in the offshore region presumably forces the tuna to rely on alternative prey – hence squid and macrozooplankton make up a greater proportion of the diet. It is unclear whether macrozooplankton are intentionally targeted, or whether they are eaten opportunistically.

Interannual differences

Overall, the relative proportions of the main prey taxa of southern bluefin remained fairly constant over the sampling period, although there were some differences in the species makeup within taxa. For example, hyperiid amphipods dominated the crustacean component in warm and intermediate waters in 1992 but were rarely eaten in the following years. At the same time, the proportion of omastrephid squid increased in the diet of offshore-caught tuna, but declined in inshore-caught fish. Some of the differences offshore may be related to an apparent transfer of longline fishing effort to the south over the study period (R. Bradford, CSIRO unpublished data). However, the increase in influence of subantarctic water off eastern Tasmania over the study period may also have altered the distribution and abundance of potential prey species. In a concurrent study we found that not only were there significant differences in the relative proportions of the major taxa with time – the proportion of fish and crustacea decreased and the proportion of gelatinous zooplankton increased – but also that the overall biomass increased (Young et al. 1996a). Unfortunately, we were unable to sample adult cephalopods adequately, and hence could not evaluate differences in their abundance or biomass between years.

Predator-prey relationships

Although there was no evidence of different-sized tuna selecting for prey size, prey taken in the inshore region were significantly larger than those offshore even though the inshore-caught tuna were smaller. Nevertheless, inshore, tuna < 90 cm ate less

fish than the larger groups, indicating that their jack mackerel prey approached the maximum size that southern bluefin < 90 cm can eat. The presence of greater proportions of salps in the diet of the largest size class of inshore-caught tuna may indicate that these larger fish are feeding closer to the edge of the continental shelf than the smaller fish.

Amongst the offshore fish, only the largest size class showed no significant diet overlap with the other sizes. The diet of these large fish contained fewer *Trachurus declivis* and larger proportions of other fish and salps. One explanation may be that they are feeding further out to sea than the smaller fish, away from the shelf and shelf break where *T. declivis* is most abundant.

Feeding behaviour

Although we found significantly more full stomachs in the morning overall, this may have been an artefact of sampling. The inshore fishery from which we took our samples operates only during daylight hours. Offshore there is some indication of a morning and evening peak in feeding, but the lack of samples around dawn limits our conclusions. Talbot & Penrith (1963) found that southern bluefin tuna fed mainly just after sunrise and again in the evening, but reported that they may also feed at night. AFZ observer records indicate that the Japanese longline fleet aim to have their lines in the water by sunrise to take advantage of the morning feeding peak (Bradford unpublished data). Peaks in feeding, in the morning and evening have been observed in a number of other tuna species. Yellowfin tuna, *Thunnus albacares*, have greatest stomach fullness between 10:00 and 11:00 h and between 15:00 and 17:00 h (Ortega-Garcia et al. 1992). A similar pattern was observed in skipjack tuna, *Katsuwonis pelamis* (Magnuson 1969). These observations are consistent with what would be expected of visual predators and probably explain why the Japanese longline fleet regard the period around the full moon as the most successful fishing period and why they set their lines earlier during a full moon (Bradford unpublished data). That most of the prey we identified have meso- to epipelagic distributions

(Young et al. 1996b) indicates that, at least off Tasmania, southern bluefin tuna are feeding in the upper layers of the water column. With the advent of 'intelligent' tags in recent times it should soon be clear whether the above hypothesis is correct.

Daily ration

Yellowfin tuna, *Thunnus albacares*, have a linear rate of gastric evacuation (Olson & Boggs 1986). However, an exponential rate of gastric evacuation, which was assumed in this study, provides a good fit to most experimental feeding data and also a good estimate of ingestion rate when used in the Elliot & Persson (1978) model (Durbin et al. 1983, Persson 1986).

Tunas are considered to have the highest metabolic rates amongst the teleost fishes, and consequently high food requirements (Bennetti et al. 1995, Dickson 1995, Olson & Boggs 1986). However, there have been few studies that have estimated the food consumption of scombrids from stomach contents data. Nevertheless, captive skipjack tuna, *Katsuwonus pelamis* eats 15% of its body weight per day (Magnuson 1969), whereas bonito, *Sarda chiliensis* eats between 2.23 and 7.04% per day (Pauly et al. 1987). Yellowfin tuna, *Thunnus albacares*, closely related to southern bluefin tuna, eats 3.9% of body weight per day (Olson & Boggs 1986). The best estimate for southern bluefin tuna – between 4 and 7% per day – was from farmed fish fed ad libitum (K. Rough personal communication). Our overall estimate of ~1% per day may have underestimated the daily ration by underestimating the rates of gastric evacuation and of digestion of prey between capture and landing in the offshore fish. However, the relatively low water temperature off eastern Tasmania could also decrease gastric evacuation, so daily ration could be expected to be lower (Durbin et al. 1983). Nevertheless, a more recent study of yellowfin tuna found that daily ration decreased as the size of the tuna increased to the extent that fish > 130 cm had a daily ration of 1% (Maladeniya 1996), which is very similar to our result.

In summary, the main feature to emerge in the feeding patterns of southern bluefin tuna off east-

ern Tasmania was the difference between inshore- and offshore-caught tuna. Our data indicated that eastern Tasmanian shelf waters are an important feeding ground for, at least, immature southern bluefin tuna on their migration through the area.

Acknowledgements

This study would not have been possible without the cooperation of the Australian Fishing Zone Observer program and the inshore commercial and recreational troll fishers of eastern Tasmania. We are also grateful for the constructive comments made by John Gunn, Cathy Bulman and Vivienne Mawson.

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CHAPTER 10

GENERAL DISCUSSION

Distribution and food chain pathways of midwater fauna off eastern Tasmania

INTRODUCTION

The waters off eastern Tasmania are home to a diverse community of pelagic fauna. Nevertheless, during the course of my studies some common themes have arisen on the relationship between this fauna, the regional oceanography and inshore/offshore processes of southeastern Tasmania. In this chapter I will draw some of these ideas together. I will then summarise the major trophic pathways operating off the east-coast of Tasmania and the variables which affect them. Finally, the types of questions that can be asked about oceanic ecosystems, are limited by the technology employed, like for all other branches of science. Here, I will summarise some of the new procedures and technologies that will help refine the types of questions we can ask and which may provide some of the answers in the future. I will also outline some of the problems which future studies may be able to address.

DISTRIBUTIONAL ECOLOGY

Introduction

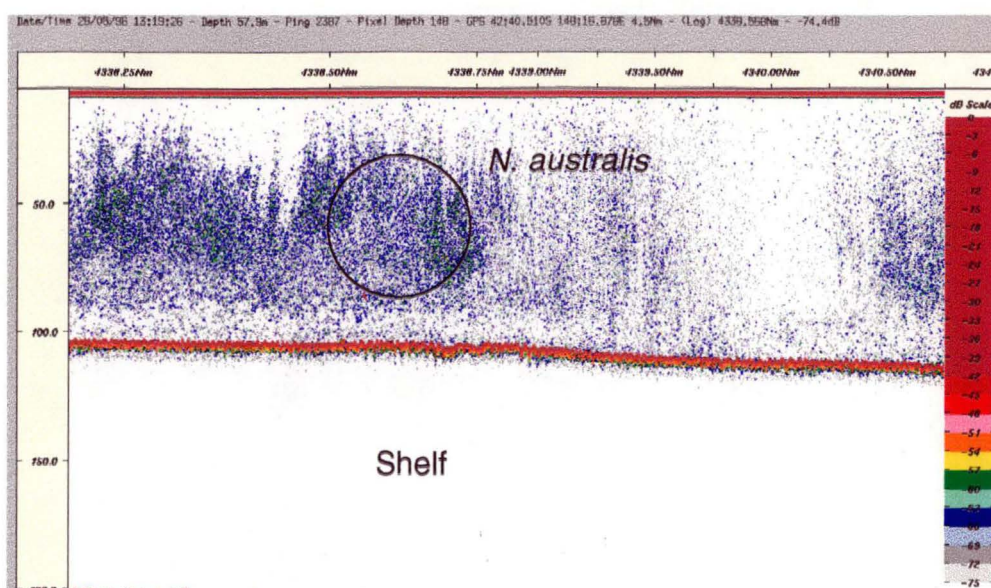
An acoustic transect heading east from coastal waters of eastern Tasmania would reveal three main depth zones. These are the shelf, ~10 n. miles wide and extending to a depth of 200 m; the upper continental slope, less than a kilometre wide and from 200 to 500 m deep and finally oceanic waters extending to depths below 3000 metres. All of these zones are far more complex in physical and biological structure than the depths that categorise them but it is a useful beginning. If we were to examine the resulting sounder traces more carefully we would see a variety of 'marks' in the midwater (Fig. 1). Although identifying these marks has its own set of limitations, the species composition of the main marks can usually be identified by net sampling, particularly for fish with swim bladders or for animals that aggregate in some way (Koslow *et al.* 1997).

Distribution and Abundance

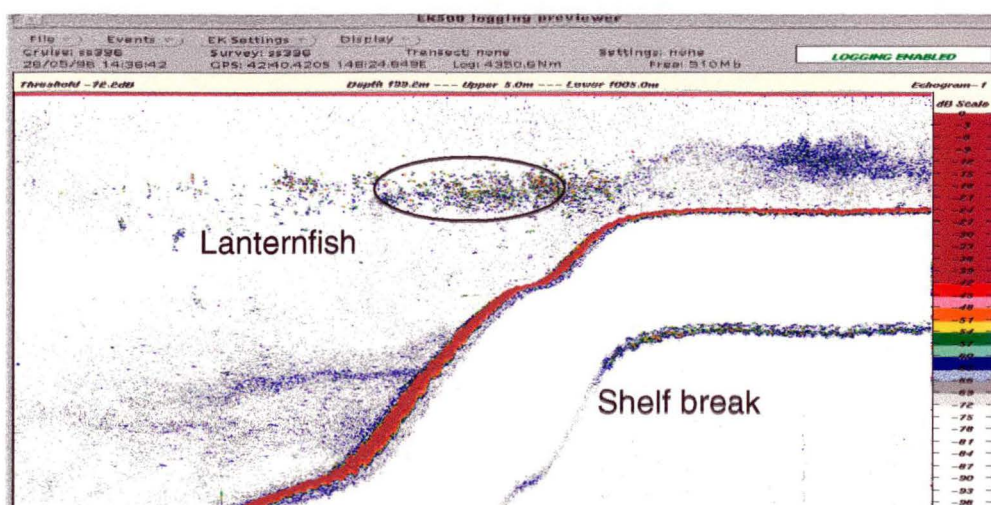
The Continental Shelf

Much of the background scatter observed on the acoustic traces on the shelf is due to zooplankton (Fig. 1). Of the zooplankton, copepods and mysids form a major part of that scatter. Earlier studies of the plankton had confirmed their importance (Nyan Taw 1975). At times, however, this background scatter will form clumps which can be readily identified as krill (*Nyctiphanes australis*), and which at times can

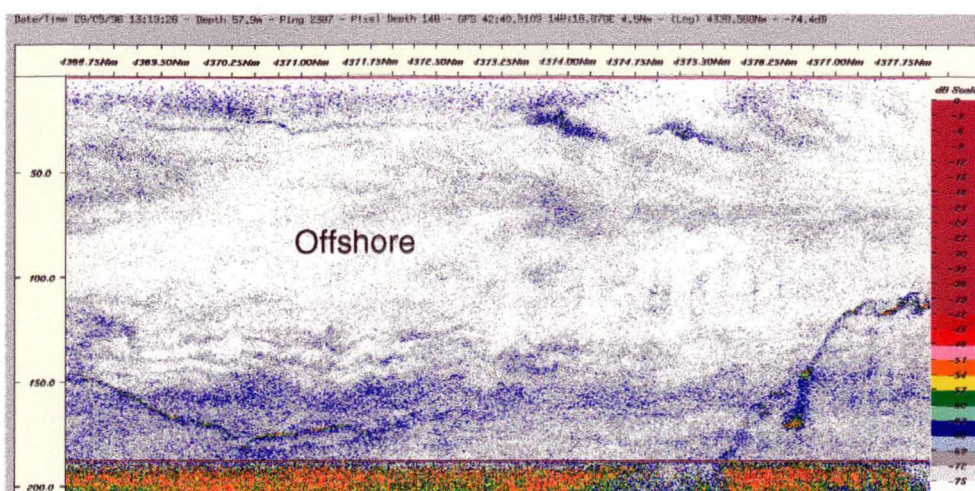
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dominate the zooplankton (see Chapter 2). Ritz and Hosie (1982) estimated that 2, 212 tonnes of this species were produced annually in Storm Bay, southern Tasmania, alone and that it had one of the highest production to biomass ratios of its kind in the world. We found that it was distributed throughout the water column and was significantly higher in biomass during autumn, presumably a response to the autumn bloom identified by Harris *et al.* (1987). Previously *N. australis* was reported to migrate vertically to surface waters at night (Blackburn 1980). In contrast we found that the “densities in many of our day surface hauls were equivalent to ...the deep haul(s)” (Young *et al.* 1993).

As we continue our observations of the acoustic trace over the shelf the small crescent shaped features can be identified as jack mackerel (*Trachurus declivis*) (Williams and Pullen 1993). This species feeds exclusively on krill when on the shelf (Chapter 2). However, part of the population moves between the shelf and the upper slope where it feeds on lanternfish (Blaber and Bulman 1987, Jordan 1994).

Example
in figure?

The Upper Slope

Continuing over the continental slope the scattering layer changes in character and intensifies due to reverberations from the swim bladders of neritic (sensu Hulley 1992) lanternfish (Fig. 1). This layer typically is found below 300 m by day rising to surface waters at night and is composed of a suite of micronektonic fishes, dominated by *Lampanyctodes hectoris*, but also including *Symbolophorus barnardi* and *Diaphus danae*, and the lightfish, *Maurolicus muelleri*. *Lampanyctodes hectoris* is usually found over a very narrow depth range (between 300 and 500 m) with echo soundings revealing their cross-slope distribution less than a kilometre in width (Fig. 1).

A central feature of this zone is the continued presence of micronektonic fishes year round, albeit with wide fluctuations in density and size structure (May and Blaber 1989, Chapter 6). For example, May and Blaber (1989) estimated the biomass of the lanternfish at 390 g.m⁻² in summer which was a seven-fold increase over their winter density. My studies of the reproduction, age characteristics and feeding (Chapters 5, 6 and 7 respectively) of this group reveal an annual cycle adapted to the seasonal fluctuations of the East Australia Current. Spawning took place in early winter in

Lampanyctodes hectoris, presumably so juveniles were of sufficient size to take advantage of increased zooplankton concentrations in spring (Chapter 5).

Maurolicus muelleri hatched later, suggesting a temporal strategy to reduce competition for food between these two species. Further separation was afforded by slightly different depth distributions — *M. muelleri* formed a band slightly higher than that of *L. hectoris* (Young, unpublished data). Differences were also measured in their diets. Over summer, when densities were highest, *L. hectoris* ate relatively more euphausiids and less copepods than did *M. muelleri*. *Diaphus danae*, another dominant lanternfish ate a large proportion of fish, mainly *L. hectoris* (Chapter 7). I concluded that feeding differences and intensity together with changes in size structure may be synchronised with seasonal variations in prey abundance to maximise the species share of the available resource. I could not determine, however, whether the winter decrease in lanternfish was due to predation or movement of the fish out of the area.

The concentration of these lanternfish over the upper slope, particularly over summer, draws other predators such as blue grenadier (*Macruronus novaezelandiae*), jack mackerel and Ray's bream (*Brama brama*) to feed on them (Bulman and Blaber 1987, May and Blaber 1989). Blue grenadier follow a diel migration up into the water column to feed on the lanternfish at night (Bulman and Blaber 1987). Further, Jordan (1994) indicated that jack mackerel movements might be in part directed by these summer concentrations over the slope.

Offshore Waters

Once past the slope the sound scattering layer changes abruptly reflecting the diffuse nature of species distributions in oceanic waters (Fig. 1). There is still a distinct scattering layer at night but this is largely composed of zooplankton. In contrast to the midwater fish community associated with the shelf and slope there is a far greater diversity of species which are again dominated by the Myctophidae, but other groups including the stomiatoids are important (Chapter 4). It should be noted, however, that this diversity refers only to the night-time distribution of these fish as most (>98%) are below 400 m by day, migrating to the surface only at night (Williams and Koslow 1997). We identified 42 lanternfish species from this region in contrast to the 19 species previously identified over the slope (May and Blaber 1989). Nektonic

species such as southern bluefin tuna, albacore, Ray's bream, and blue sharks, however, are regularly found in surface waters by day.

Inshore/Offshore Relationships

Although the above species are generally found within their respective zones, migrations between the shelf and offshore are known for jack mackerel (Jordan 1994), southern bluefin tuna and possibly squid (*Nototodarus gouldii*) (see Chapter 9). Jordan (1994) proposed that jack mackerel move from the shelf to spawn on the shelf break in the Austral spring. Also, although *Nyctiphanes australis* is normally confined to the shelf, flooding of the shelf and subsequent runoff offshore in at least 1989 extended its distribution offshore (F. B. Griffiths, CSIRO unpublished data). Southern bluefin tuna migrates from the waters of the Great Australian Bight in autumn and overwinters in the waters surrounding Tasmania, apparently in response to increased prey levels. During this time it moves freely between inshore and offshore waters, to feed (Chapter 9). Albacore tuna (*Thunnus alalunga*), which arrive from the north slightly before southern bluefin tuna in March (J. Young, Pers. Observ.), appear to concentrate along the 100 m depth contour and feed entirely on krill during their stay.

Seasonal and Interannual Variations

Overlying these basic patterns of distribution are those generated by seasonal and interannual differences in the regional oceanography. These changes are largely attributed to large-scale events such as the El Nino southern oscillation (Harris *et al.* 1987) although more recent studies suggest that such variations between years were correlated with the position of the mean high-pressure ridge (Thresher 1994). Whatever the mechanism it appears that it is the relative strength of warm tropical water compared to cooler subantarctic water that determines the relative contribution to the overall species mix in the area. The annual fluctuations in krill stocks off eastern Tasmania between 1989 and 1991 are but one example (Chapter 2). Earlier reports by Blackburn (1957) of fluctuations in the catch of barracouta (*Thyrstites atun*) indicate that these cycles are not new to the area. A more recent example is the appearance of large numbers of yellowfin tuna and some marlin off northeastern Tasmania (N. Harper, NE Tas. Fisher) over the last two summers in response to a strong anti El nino flush of East Australia Current down the east coast of Australia. Recreational fishers from the north east coast of Tasmania recall years when

yellowfin catches were high, offshore waters were unseasonably warm (Whitelaw *et al.* 1996). The domestic longline fishery off Eden (southern NSW) is recently becoming attuned to take into account these cycles when planning their fishing programs (Joy Puglisi, Eden tuna fisher, Pers. Comm.).

TROPHIC RELATIONS

Introduction

Over the period of this study I have investigated the feeding ecology of fish from shelf, slope and offshore waters. There is also a growing literature on other species in the region that I will draw on. Here I will develop an overall picture of the feeding pathways of these areas and their interrelationships. Blaber and Bulman (1987) identified five feeding guilds from the upper slope alone. As I am dealing with the midwater I have taken a slightly different approach and have also isolated the major prey categories. Some of my conclusions differ from that of Blaber and Bulman (1987). For example, they describe jack mackerel as pelagic piscivores, whereas my analyses indicate that they spend a far greater time on the shelf eating krill and are thus omnivorous.

On the shelf the diets of krill (Ritz *et al.* 1982) and larval and adult jack mackerel (Chapters 2 and 8) have previously been described. Over the slope the diets of the pelagic lanternfish, lightfish and their main predator blue grenadier have also been described (Chapter 7, Bulman and Blaber 1986), as have the main demersal species of the upper slope (Blaber and Bulman 1986). Deeper down the slope the diet and energetics of orange roughy have also been examined (Bulman and Koslow 1992). The diets of some of the common midwater species offshore have also been described (Young *et al.* 1994). More recently a survey of the feeding ecology of deep-water midwater fishes off southern Tasmania has begun (A. Williams, CSIRO unpublished data). The feeding ecology of southern bluefin tuna has been described for both inshore and offshore waters (Chapter 9).

I have summarised the main trophic pathways operating in the midwater off eastern Tasmania in Figure 2. In it I identify the main groupings (see also Table 1), which I will summarise below. However, these groups could have been divided further (*eg.* within the neritic lanternfish there is a distinction between lightfish (*Maurolicus muelleri*) and lanternfish and so on (see Chapter 7). I have also summarised the

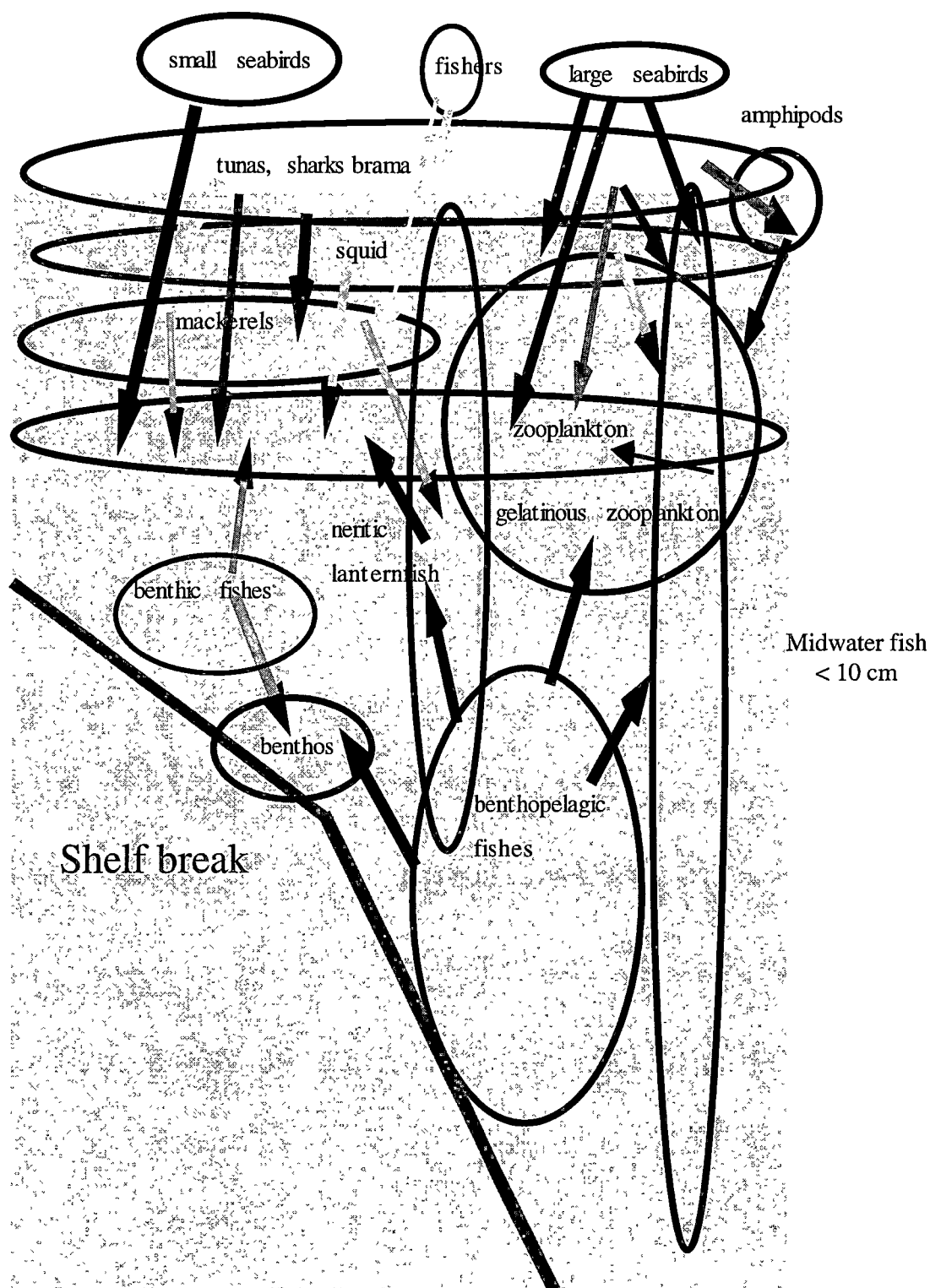


Figure 2 Schematic diagram of the main species groups off eastern Tasmania: their distribution and trophic links (not drawn to scale)

main prey categories. Not depicted in the figure but underlying these trophic relationships is the phytoplankton stock which, at the shelf break at least, follows a

strong seasonal pattern with two peaks, one in autumn and another in spring (Harris *et al.* 1987). These peaks appear to drive the seasonal cycles and species successions in the area.

Table 1: The main trophic and prey categories with representative species from inshore and offshore waters off eastern Tasmania

Trophic category	Species
Large pelagic omnivores	<i>Thunnus maccoyii</i> , <i>Isurus oxyrinchus</i>
Pelagic omnivores	<i>Trachurus declivis</i> , <i>Emmelichthys nitidus</i>
Pelagic piscivores	<i>Brama brama</i>
Small mesopelagic omnivores	<i>Diaphus danae</i> , <i>Lampanyctus australis</i> and <i>Chauliodus sloanii</i>
Neritic planktivores	<i>Lampanyctodes hectoris</i>
Squid	<i>Nototodarus gouldii</i>
Gelatinous zooplankton	<i>Pyrosoma pyrosoma</i>
Inshore and offshore zooplankton	<i>Pleuromamma</i> spp., <i>Phronima sedentaria</i> , <i>Nyctiphanes australis</i>
Bathypelagic omnivores	<i>Hoplostethus atlanticus</i>

Prey Categories

Inshore and Offshore Zooplankton

Crustacea within this group are particularly important in the food web off eastern Tasmania as they lead, either directly or indirectly, to almost all the organisms higher in the chain. Across the shelf and seaward there is a broad group of zooplankton species feeding on the algae, detritus and on other zooplankton species (Nyan Taw 1975, Ritz *et al.* 1990). They can be broadly divided into shelf and offshore species but with many overlaps. Over the shelf calanoids, and euphausiids (dominated by *Nyctiphanes australis*) are the main taxa present although *N. australis* figures most prominently in the food chain for both fish and seabirds (Chapter 2). Larval fishes on

the shelf, dominated by those of jack mackerel, feed largely on copepods but callyptopid stage *N. australis* are common prey (Chapter 8).

Over the slope the mix of euphausiids to calanoids is more even, and their importance as prey more dependent on the season. For example, in the lanternfish *Lampanyctodes hectoris* euphausiids dominated as prey over summer whereas calanoids dominated in winter (Chapter 7). Offshore *Pleuromamma* spp. is the main prey species for many of the mesopelagic species. Hyperiid amphipods (particularly *Phronima sedentaria* but also *Phrosina semilunata* and *Brachyscelus cruscum*), which graze on gelatinous zooplankton (Laval 1980), are prominent in the diet of southern bluefin tuna (Chapter 9).

Gelatinous Zooplankton

Perhaps the group that is least understood in terms of trophic position is the gelatinous zooplankton — largely because they are difficult to sample in the wild. For one, the fragility of gelatinous zooplankton makes them very difficult to sample quantitatively using nets. There is also the perception that these “jellies” have low nutritional value and therefore are not important in the food web despite the growing literature to the contrary (eg. Kashkina 1987, see also Deibel 1998). For one, although they have a high water content, on a dry weight basis they contain a relatively high proportion of nitrogen. As such, the distribution, biomass and trophodynamics of gelatinous zooplankton have yet to be effectively addressed, although recently they are receiving more attention (eg. Pages *et al.* 1996). My study found that at least for the larger, more robust species (eg. *Pyrosoma atlanticum* and *Thetys vagina*), they are a major part of the midwater fauna — the biomass of gelatinous zooplankton was consistently over 50% in two of the three years we sampled it (Chapter 3, Fig. 4). Pages *et al.* (1996) found even higher biomasses in the Southern Ocean and proposed that their importance increased in years when krill populations were low. Off Tasmania they were eaten by southern bluefin tuna, trevalla (*Hyperoglyphe atlanticum*) and benthopelagic species such as *Helicolenus percooides* and *Neocyttus rhomboidalis* feed on them (Chapter 9, Blaber and Bulman 1987). We also know that hyperiid amphipods, an important prey of southern bluefin tuna, make their home on or in this group (Laval 1980). Their importance as prey is well known. However, their role as predator is less clear (Parsons 1991), although

studies elsewhere have shown that they feed on zooplankton and juvenile fishes (Swanberg and Bamstedt 1991).

Cephalopods

The problem for squid is perhaps the reverse of that for the gelatinous zooplankton. We know they are central to the food chain off eastern Tasmania, particularly for larger fish predators such as southern bluefin tuna (Chapter 9). However, because of their ability to avoid nets, they are difficult to quantify. According to our biomass data they are a very small part of the midwater fauna (Chapter 3). However, they are one of the most important preys of southern bluefin tuna and sharks (Chapter 9, Young unpublished data on sharks), and the presence of beaks in most stomachs of these top predators indicates they are a continuing feed source.

Little is known of the diets of cephalopods because of the thoroughness with which they break down their prey during feeding (Dr. C. C. Lu, Museum of Victoria, Pers. Comm.). In Tasmanian east coast waters, cephalopods in the 10 to 50 cm class are dominated by southern arrow squid (*Todarodes filipovae*), and Gould's arrow squid (*Nototodarus gouldi*). Both species eat mainly pelagic fish in the 2–10 cm size range, cephalopods in the 2–10 cm size range and pelagic crustacea less than 2 cm (O'Sullivan and Cullen 1983, Dunning and Brandt 1985). Cephalopods in the 2–10 cm size range such as *Abraliopsis gilchristi*, *Lycoteuthis lorigera* and paper nautilus (*Argonauta nodosa*) prey on pelagic crustacea less than 2 cm, particularly euphausiids.

Trophic Categories

Fish <10 cm

This group includes small mesopelagic omnivores such as the lanternfish *Diaphus danae* and neritic planktivores such as *Lampanyctodes hectoris* and *Maurolicus muelleri*. Small piscivores (eg. *Chauliodus sloanii*) are also found in this group.

Lanternfish, the main component of this group, are not found over the shelf. However, there is a group of lanternfish associated with the continental slope, the diets of which I examined in Chapter 7. There is a marked seasonal component to the diet of the slope lanternfish — they feed largely on euphausiids in summer and copepods in winter. Offshore, *Lampanyctus australis*, *Lampichthys procerus* and

Diaphus danae were the three most abundant species of lanternfish (Chapter 4). Their diets were dominated by crustacean zooplankton, particularly species of the calanoid genus *Pleuromamma*, which was a dominant zooplankton species in the study area (Young *et al.* 1994). Cyclopoid copepods, ostracods and euphausiids were also important as prey. There were some small differences: gastropods were common in the stomachs of *D. danae*, whereas fish scales were common in the stomachs of *L. australis* and *L. procerus*. However, most prey were in the size range of 1 to 3 mm total length, reflecting the importance of calanoid copepods, particularly *Pleuromamma* spp., in the diets of these species.

Unlike some offshore (usually tropical) communities (*eg.* Macpherson 1988) lanternfish in Tasmanian waters do not provide a direct link to top predators such as tuna. Many of these top predators feed during the day, when most of the mesopelagic descend to depths below 300 m (Karnella 1987). At night, when the mesopelagic fish migrate to surface water, potential predators tend to be feeding less. For these reasons mesopelagic fish generally make up only a small proportion of the diet of larger pelagic fish (Roger and Grandperrin 1976). However, pelagic cephalopods and some species of pelagic fish, notably Ray's bream (*Brama brama*), which are prey for the tuna do prey on mesopelagic fish (Gjøsaeter and Kawaguchi 1980, Blaber and Bulman 1987, this study). Therefore, either directly or indirectly, myctophids underpin the food web of many larger pelagic species.

Non-mycetophids <10 cm

The stomachs of *Howella sherboni* and *Diretmus argenteus* were dominated by crustacean zooplankton, particularly species of *Pleuromamma*. *Chauliodus sloani* was entirely piscivorous, feeding mainly on small (<50 mm SL) lanternfish (Young *et al.* 1994). Although not generally as abundant as the myctophids this group fill a similar position in the food chain. Many of these species have relatively deep vertical ranges and therefore are also prey to deeper living species such as orange roughy (Bulman and Koslow 1992).

Pelagic Fish 10 to 50 cm

This group includes the pelagic omnivores (*eg.* *Trachurus declivis*) and pelagic piscivores (*eg.* *Brama brama*). Among the most common pelagic fishes in this size range off the Tasmanian east coast are jack mackerel (*Trachurus declivis*), Ray's

bream (*Brama brama*) and redbait (*Emmelichthys nitidus*). Jack mackerel feed exclusively on krill (*Nyctiphanes australis*) over the continental shelf, but feed on lanternfish (*Lampanyctodes hectoris*) over the continental slope (Blaber and Bulman 1987). Redbait off the coast of South Africa eat a very similar range of prey (Meyer and Smale 1991). Ray's bream fed on squid and fish in the 2–10 cm size range; particularly on lantern fish. They also fed on pelagic crustacea < 2 cm size, particularly pelagic amphipods (Blaber and Bulman 1987, Young *et al.* 1994).

Large Pelagic Omnivores

Off eastern Tasmania the main top predators are tuna (mainly southern bluefin tuna but also albacore and yellowfin tuna), and sharks (mainly blue sharks *Prionace glauca* but also shortfin mako sharks *Isurus oxyrinchus*). The diet of southern bluefin tuna was dominated by fish and squid between 10–50 cm in size (Chapter 9). However, pelagic crustacea (particularly amphipods) <2 cm were also important. Prey were commonly surface or epipelagic in distribution, and some, such as jack mackerel and juvenile Gould's arrow squid (*Nototodarus gouldi*), were typically associated with the continental shelf. The diet of the main oceanic sharks is very similar to that of southern bluefin tuna consisting mainly of pelagic fish, squid and crustacea (Stevens 1984, J. Young, unpublished data).

Bathypelagic Omnivores

Orange roughy (*Hoplostethus atlanticus*) is a deepwater species living below 700 m depth (Bulman *et al.* in press), and is therefore below the depth range of this study. However, as its diet includes many of the micronekton species that spend their daytime at depth, information on its trophic relations is appropriate. Although orange roughy feeds on fish, crustacea and squid, the species mix is quite different to that eaten by mid- to epipelagic feeders such as southern bluefin tuna. For example, myctophid (eg. *Lampichthys procerus* and *Lampanyctus* species) and stomiatoid fishes (eg. *Chauliodus sloani*), rare in the diet of southern bluefin, are eaten by orange roughy. Similarly, deepwater crustaceans (eg. *Acantheephyra pelagica* and *Gnathophausia ingens*) are absent in the latter but are common prey of orange roughy (Bulman and Koslow 1992). No predators of orange roughy (excluding fishers) have been identified (C. Bulman, CSIRO Pers. Comm.).

The Seabed

This thesis has concentrated mainly on the midwater fauna off eastern Tasmania. However, there is a complex and species-rich fish fauna inhabiting the seabed from the shelf to well below 1000 m. As yet there is little data on trophic relationships on the shelf (although see Chapter 2). However, a recent study of demersal fish on the shelf found significant variations in biomass between years (Jordan 1997). Jordan attributed these differences to interannual variations in the regional oceanography driving changes in coastal productivity.

The interactions of the demersal fish fauna of the upper slope, however, have been well documented by Blaber and Bulman (1987). They identified four trophic categories — pelagic piscivores, epibenthic piscivores, epibenthic invertebrate feeders and benthopelagic omnivores. Underwater photography also revealed areas of seabed on the upper slope covered in ophiuroids (brittle stars) with their own suite of predators (eg. *Centriscops humerosus*) (Blaber *et al.* 1987).

Seabirds

Large seabirds such as shy albatross (*Diomedea cauta*) eat a very similar range of prey to pelagic fish greater than 50 cm. Gales (1993) lists fish, cephalopods and crustacea as important in their diet. The diet of small seabirds such as fairy prion (*Pachyptila turtur*) and shearwater (*Puffinis tenuirostris*) has much in common with the diet of fish in the 10–50 cm size class. Both species eat mainly euphausiids, as well as small fish and squid (Marchant and Higgins 1990).

“Bottom Up” Versus “Top Down” Effects

In the introduction to this thesis I mentioned the perspective offered by Harris and Griffiths (1987) that “bottom up” rather than “top down” effects were important determinants of community structure in the waters off eastern Tasmania. This follows the general view that there is a relationship between fish production and food production (Mann 1993). To an extent this study supports that view (eg. see Chapter 2). However, one possible hypothesis for the disappearance of lanternfish from the shelf break in winter could have been through massive predation by larger species such as blue grenadier and jack mackerel (Bulman and Blaber 1987), supporting the idea of a trophic cascade. As the lanternfish in this case is one of the few species in these waters restricted in their distribution such an hypothesis is plausible. However,

as zooplankton biomass decreases during this period it may be that there was insufficient food to support dense aggregations of lanternfish. Perhaps, in such an open-ended system, there is room for both positions. In any case, it may be that the impact of such effects is more subtle, particularly as the east coast of Tasmania is only a temporary home for top predators such as tuna. For example, it may be that changes in primary production — through variations in the regional oceanography — may be reflected more in the condition of these temporary inhabitants, rather than in more absolute terms such as mortality. Anecdotal accounts are certainly reported (as yet unquantified) by tuna fishers of catches of tuna that in some years are in “good” (fat) condition but in other years are in “poor” condition (W. Whitelaw, CSIRO, Pers. Comm.).

Summary

The food chain off eastern Tasmania is best described as a number of separate ones, linked to water depth and substrate, but also linked horizontally by larger, mobile predators such as southern bluefin tuna. Vertically, these chains can be linked by benthopelagic predators such as blue grenadier and vertically-migrating midwater fishes and crustacea. Further, the diurnal migrations of some of these groups place them in a pelagic food web during the night and a demersal food web during the day. Consequently energy from epipelagic production, passing through these mesopelagic species, may be retained in surface waters or passed into deeper waters.

COMPARISONS WITH OTHER AREAS

The intriguing feature of the species mix in the upper 400 m of the water column off eastern Tasmania is the similarity it holds with other southern and northern hemisphere near-shore environments. For example, off South Africa although the main krill species is *Nyctiphanes capensis*, the main myctophid is *Lampanyctodes hectoris*, and mackerel (in their waters *Trachurus trachurus*) and southern bluefin tuna are also common (Crawford 1980). Off New Zealand the krill species is *also* *N. australis* but the mackerel is *T. murphyi* (Jones 1990). Off California yet another species of *Nyctiphanes* — *N. symplex* — is prey for larger predators including albacore tuna *Thunnus alalunga* (Fiedler and Barnard 1987), also a common species off eastern Tasmania. All of these areas are washed by boundary currents and in the southern hemisphere are greatly influenced by the position of the subtropical convergence (eg. Pakhamov *et al.* 1994). Therefore, the relationships and patterns

demonstrated in the present study, and their links to top predators such as SBT, can have far wider applications than just for the east coast of Tasmania.

Of more immediate interest to me, however, are the parallels that can be drawn from this study to other areas along the Australian coastline through which species such as southern bluefin tuna pass. We know a good deal about the movements of southern bluefin in the Australian Fishing Zone but apart from the studies off eastern Tasmania there is little information on why the tuna aggregate in the places they do. For example, there are “staging grounds” for southern bluefin off southeastern NSW and the Great Australian Bight (GAB). Are these areas feeding grounds for the tuna or are they there for some other reason? In the case of the GAB it has been suggested that the tuna use the shelf waters as a thermal refuge — the region is dominated by the warm extension of the Leeuwin — from which they make forays into the colder, more productive surrounding waters to feed. I have just led a cruise (Southern Surveyor Cruise 1/98) to the Bight where one of our objectives was to examine the biological basis for tuna aggregations in the area. Preliminary analyses show little potential prey where the fish concentrate — and are fished. However, significant amounts of potential prey were found over the shelf break or inshore around the many reefs and islands (Young in preparation). The hope in the future is to develop a model of the movements and trophodynamics of southern bluefin tuna in the Australian Fishing Zone. Understanding the relationships between tuna and prey stocks will take on considerable importance if we find cross linkages with other fisheries. For example, our preliminary study in the GAB found that inshore and shelf-break waters had large amounts of potential feed such as the pilchard *Sardinops neopilchardus*. As this species supports a fishery in its own right understanding the impact of SBT on it takes on special significance.

SAMPLING LIMITATIONS AND SOME NEW STRATEGIES

Brandt (1981) listed a number of limitations to a study he did on the midwater fishes associated with a warm core eddy off eastern Australia. These limitations included small sample sizes due to gear avoidance and escapement, gear bias influencing the type and size of fish caught, the lack of an adequate opening-closing net system and limited temporal coverage (ship time is very expensive!). Brandt’s comments in that paper illustrate the technical difficulties encountered in studying deepwater environments and echo earlier comments by Angel (1977). The latter proposed that

each sampler offered only a “limited window into the spectra of variability”. Further, manipulative studies of the deep oceans, similar to those done in near-shore environments (eg. Underwood *et al.* 1983), are not generally feasible. In that sense, progress in the study of deepwater ecology, it could be argued, has lagged behind. However, it is becoming apparent that the proper management of many fisheries will depend in some part on an understanding of the physical and biotic environment in which they are found. Below I will report on some of the more recent advances that I have been involved in, and which have added to my understanding of the systems I have studied. I will also comment on areas where more work or different strategies are needed. Some of the most important developments in recent times are those in acoustics and electronics. However, as very little of my work has dealt with these areas of research I will not discuss them here.

Sampling Techniques

Lack of replication is perhaps one of the most confounding problems faced by biologists working in deep water. Ship time is expensive and thus restricted and if bad weather coincides with the timing for a particular piece of research then the number of samples usually suffers. Therefore, it is necessary to devise sampling programs that can be replicated but that can be performed quickly so that ship time is not too lengthy. There have been considerable advances in net technology, particularly in plankton nets, which have gone some way to address this problem. The more frequent use of multiple net systems such as the MOCNESS and BIONESS systems (Weibe *et al.* 1976, Sameoto *et al.* 1982) has revealed a great deal of information on the vertical distribution of midwater fishes and zooplankton. However, the horizontal distribution of these species can be confounded by limited sampling with few replicates (Brandt 1981). The problem of patchiness in ocean environments has been dealt with at length (Omori and Ikeda 1984). In a separate study of larval southern bluefin tuna we found that too few samples can have a dramatic effect on our understanding of their distribution (Davis *et al.* 1990). In Chapter 3 I described a system of sampling which enabled replication of samples for the estimation of macrozooplankton biomass in different water masses. A plankton (bongo) net was deployed over a grid of small area ($\sim 5 \text{ km}^2$) and towed obliquely for 20 minutes (Young 1994). This technique enabled us to sample as many as twenty times in the same water mass in less than a day giving us statistically useable numbers of samples to compare, in my case, the relative biomass of different water

masses (Chapter 3). Using one type of net, however, provides only a limited view of the midwater fauna present. I found that by using a series of net types and sizes it was possible to develop a broader picture of distribution and abundance of the midwater fauna.

Net Technology

One of the greatest advances in understanding the distribution in space and time of oceanic fauna is the development of nets which can simultaneously sample different depths. Although they have been used in northern hemisphere studies for some time their use in Australian research has been slow, largely with the difficulty in making the various systems work. Earlier studies I have been involved in were greatly limited by this fact (Young and Anderson 1987, Young 1989). For example, the modified RMT 1+8 (Griffiths *et al.* 1980) was an efficient sampler but the electronics designed to open and close the net rarely worked (Brandt 1983).

However, in recent years I have been involved in the use and development of a midwater sampling device, the 'Midoc' net (Percy *et al.* 1977), which has allowed us to begin developing a three dimensional view of the midwater fauna. To my knowledge the vertical distributions presented in Chapters 3 and 4 are the first published accounts for midwater fishes in Australian waters that were not 'contaminated' by fauna from above the depth at which the sample was taken.

We need, however, to encourage the use of standard nets by deepwater ecologists. Much the same as oceanographers apply strict practices for sampling the midwater we will need to standardize our own systems of collecting otherwise the opportunity of building up a coherent view of the midwater will be confounded by the biases of the various nets in use.

Other Sampling Technologies

The use of nets, however, will always be hampered by such factors as avoidance and escapement by animals either smaller, faster or larger than for which the net is designed. For example, Daly and Macaulay (1988) found that net catches of *Euphausia superba* were only 4% of acoustic estimates. Further, for some groups such as cephalopods, nets capture only the smaller or slower species. The prominence of squid in the stomachs of southern bluefin tuna (Chapter 9) and their scarcity in net samples off eastern Tasmania (Chapter 3) supports this conclusion.

There is a requirement, therefore, for other ways of sampling the midwater fauna. One development in recent times has been the use of ‘intelligent’ tags on large predators to determine not only their patterns of movement and behaviour, but those of their prey. One of these tags, the ‘archival’ tag, which is being developed by CSIRO, is giving us extraordinary insights into the movement and behaviour of southern bluefin tuna. Combined with more traditional techniques such as those employed on research vessels our understanding of many species will grow enormously over the next few years. For example, in May 1994 a southern bluefin tuna with an archival tag (J. Gunn, CSIRO, pers. Comm.) swam through the waters of eastern Tasmania at the same time we were sampling these waters from FRV Southern Surveyor (see Chapters 3 and 4). Although only preliminary data are available, we are “ground-truthing” the movement of the tuna using physical oceanographic data from that research cruise.

Taxonomy of Species or Size?

The taxonomy of midwater fish and zooplankton, although improving, is not well documented for Australian waters and the number of trained taxonomists is small. Added to this the length of time needed for species identification it is rarely possible to identify all that is in the samples, particularly in the case of the zooplankton. However, one of the constants that keeps appearing in this study was the importance of size, as opposed to the recognition of individual species (although species such as *Nyctiphanes australis* [Young *et al.* 1993] and *Lampanyctodes hectoris* [Young and Blaber 1986] are exceptions off Tasmania), in understanding ecosystem interactions. For example, a proportional increase in macro- over microzooplankton is usually found in nutrient enriched waters (Bays and Crinsman 1983). By measuring the size structure of the main zooplankton taxa, rather than the more lengthy identification of individual organisms, water productivity or lack thereof can be determined quickly. To this end we have been investigating the use of silhouette photography (Davis and Weibe 1985) to investigate differences between different water masses off the coast of southeast NSW (Berry and Young in preparation).

Ocean Colour

Satellite imagery is an important tool in understanding the processes leading to aggregations of fish (*eg.* Laurs *et al.* 1984, Fiedler *et al.* 1984). Initially, these satellites provided large-scale views of surface temperature that could be linked to

fish distributions. Further refinement led to the ability to detect “ocean colour”, a measure of the amount of chlorophyll, and hence productivity, in the surface waters of the world’s oceans (Smith 1981, Longhurst *et al.* 1995). However, even though ocean colour has been in existence in the northern hemisphere for some time it has yet to be used consistently in Australia waters. I am presently involved in a project that will aim to link recently available ocean colour data with catches by the longline tuna fisheries scattered along eastern Australia. Its use will greatly improve our understanding of the productivity of ocean currents in the Australian region, particularly off eastern Australian. A spin-off from this work is the development of an underway sampler for fluorescence originally designed to calibrate the satellite imagery. We have just deployed two of these systems on tuna longline vessels working off the NSW coast.

Long Term Monitoring

With all the developments and advances in recent times in Australian marine science there are still some glaring omissions and, for me, one of the greatest is the lack of long term monitoring stations of physical and biological parameters around the coast of Australia. The Maria Island station off eastern Tasmania is the only long term monitoring station on the east coast of Australia. It has been running for nearly 50 years and measures physical parameters (Harris *et al.* 1987). However, nowhere around Australia are such long term data sets for plankton available, even though there is a perception that “fluctuations in fish stocks are linked, via the plankton, to climatic variation” (Harris and Griffiths 1987, see also Polovina 1996). The value of long term monitoring has been proven in the northern hemisphere in many instances where failure of pulses of particular “indicator” zooplankton species, particularly of copepods, have been linked to recruitment failures in a number of commercial fisheries (*eg.* Cushing 1982). The value of such long-term studies was highlighted by a thirty year investigation of California zooplankton which showed that interannual variability in plankton abundance was greater than that between seasons (Chelton *et al.* 1982).

Closer to home, a recent study of twenty years of Antarctic krill data (funded from the northern hemisphere) proposed a complex and innovative model of krill recruitment dynamics, which would not have been possible without a lengthy time series (Siegel and Loeb 1995). It could be argued that with the global coverage of

sea-surface temperatures by satellite imagery, and our growing understanding of cyclic processes such as the El nino, the use of indicator plankton species is redundant. However, the recent example of the mass pilchard mortality around Australia, and the mystery as to why it occurred, highlighted our lack of long term knowledge of changes in prey fields. In fact, a research cruise initiated to examine the phenomenon had as one of its objective to sample the plankton to test whether starvation was a possible cause of the mortalities (Griffin *et al.* 1997). Ironically, the long term study referred to above off California (Chelton *et al.* 1982) was begun in response to fluctuations in the local sardine fishery. The failure again last year (1997) of the jack mackerel fishery off eastern Tasmania may have been predicted if sampling of the plankton had continued. We are presently examining samples taken on a voyage around Tasmania by RV Franklin during this period (Bradford and Young in preparation). Preliminary results indicate a similar scenario to that found in 1988/89 (Chapter 2). That is, water temperatures above 16°C over the shelf led to the disappearance of krill.

The reasons for the lack of these long-term studies have a great deal to do with the way research funding is allotted presently, usually on a three-year cycle. As institutional funds are in short supply and the benefits of long term studies is just that — long term — it will take a shift in emphasis from the present-day culture of user pays before a commitment to longer term projects such as these is possible.

CONCLUSIONS

Although the earlier studies in this thesis were concerned mainly with single species it soon became clear that there was a great deal of interconnection between them, underlain by strong seasonal and interannual oceanographic cycles, off eastern Tasmania. The link between inshore and offshore was of similar importance. The latter studies, therefore, have been concerned with exploring these connections, particularly in relation to the commercial fisheries in the area. The relevance of two of these studies are outlined below.

The first of these studies showed the link between fluctuations in the strength of the East Australia Current, and the availability of jack mackerel to the fishery — a flush of warm water generated by a major anti El nino (or La nina) event led to the disappearance for a time of its main prey, *Nyctiphanes australis* (Young *et al.* 1993).

Understanding these patterns has important implications for the management of the jack mackerel fishery. Monitoring of the species composition of the zooplankton of the east coast of Tasmania in relation to the physical oceanography could lead to predictive models of potential catches of jack mackerel.

The second series of studies (Young *et al.* 1996a & b, Young *et al.* 1997) revealed the importance of shelf and slope waters to populations of southern bluefin tuna off eastern Tasmania. Previously, the front separating tropical and subantarctic waters was seen as the main reason for concentrations of southern bluefin tuna off eastern Tasmania during autumn (Shingu 1980). However, my studies indicated that it was the shelf that provided an important prey source, mainly jack mackerel, for the tuna. As management of the jack mackerel is the responsibility of the state while the federal government is responsible for tuna, effective management must include dialogue between the two.

The close ecological linkages between these two fisheries supports the notion then of devising wider, discipline-based studies which have as their goal linking the physical and biological environment with top-order predators, particularly when the latter are the focus of commercial fisheries.

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