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 sagittale were examined under the light microscope (6 × 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 × 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
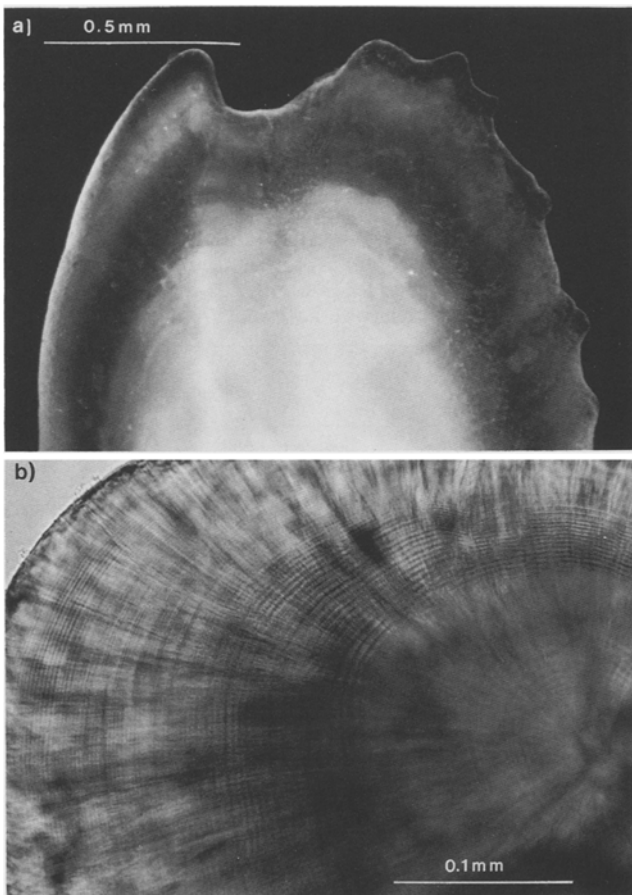
Fig. 1. *Lampanyctodes hectoris*. (a) Sagitta of an Age 1+ fish; (b) lapillus of a 100 d-old fish. (Both light micrographs)

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 interanually.

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 ($\bar{x} = 22.2$,
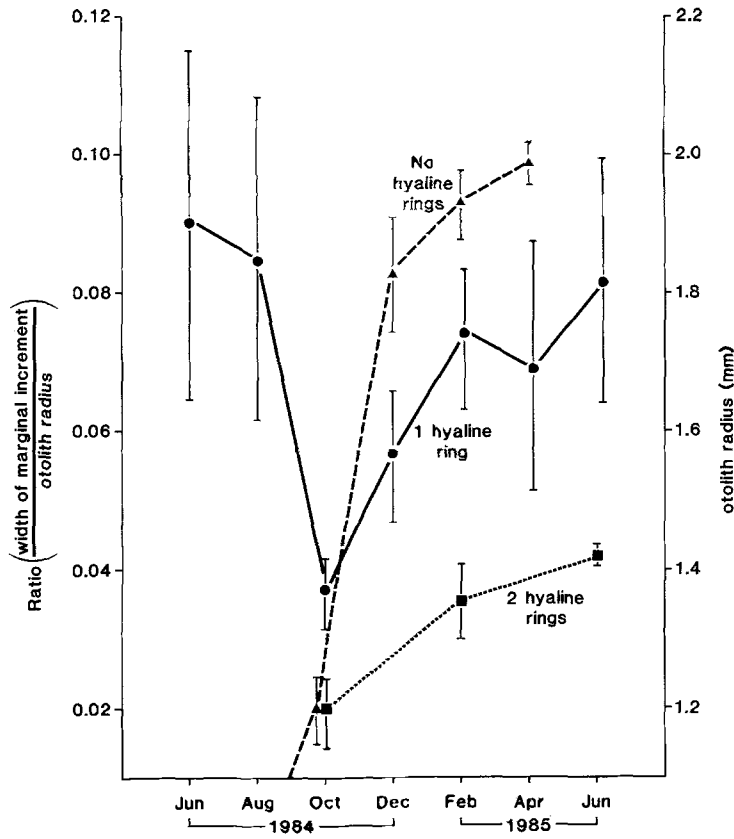
Fig. 2. *Lampanyctodes hectoris.* Seasonal changes in marginal increments (expressed as ratio of width of marginal increment to otolith radius) of sagittae of Age 1+ and 2+ fish (left-hand axis). Right-hand axis refers to increase in otolith radius of fish with no hyaline ring present (±2 SE)
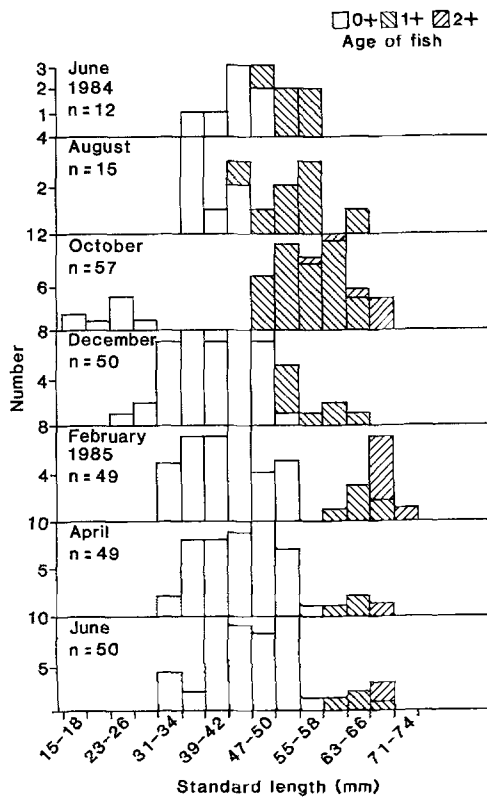

Fig. 3. *Lampanyctodes hectoris.* Length-frequency distributions of Age 0+, 1+ and 2+ fish, derived from otolithic ageing
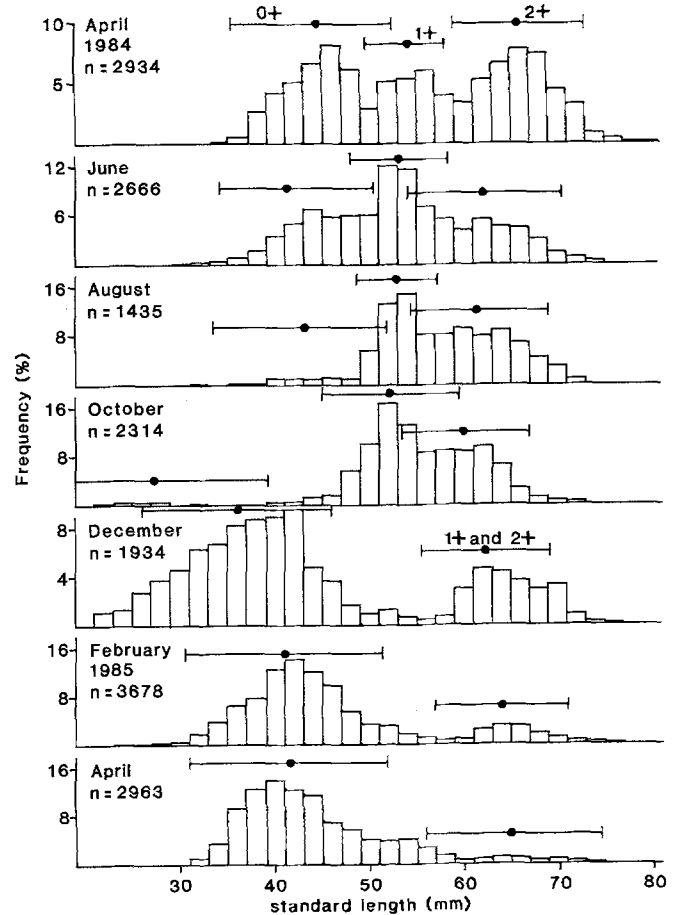

Fig. 4. *Lampanyctodes hectoris.* Length-frequency distributions of fish sampled between April 1984 and April 1985 off eastern Tasmania (±2 SE)

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)	
	S	4.39 (0.16)	2.20 (0.40)	3.78 (0.14)	6.7 (3)
	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)	
	S	4.39 (0.31)	2.73 (0.43)	4.34 (0.35)	4.3 (3)
	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)	
	S	4.51 (0.91)	2.03 (0.22)	3.47 (0.27)	4.7 (3)
	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)	
	S	6.68 (1.25)	3.77 (0.22)	3.47 (0.27)	82.7 (5)
	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)	
	S	5.05 (0.07)	3.28	(0.57)	6.9 (2)
	P	0.75 (0.01)	0.25	(0.01)	
1985					
Feb.	$\bar{x}$	41.32 (0.09)	64.31	(0.67)	
	S	5.05 (0.07)	3.28	(0.57)	67.2 (7)
	P	0.95 (0.02)	0.05	(0.01)	
Apr.	$\bar{x}$	42.57 (0.16)	64.36	(1.01)	
	S	5.04 (0.11)	4.50	(0.67)	67.2 (7)
	P	0.95 (0.02)	0.05	(0.01)	
June	$\bar{x}$	46.27 (0.11)	65.84	(0.32)	
	S	5.24 (0.09)	2.58	(0.26)	157.7 (6)
	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:

$$y = 26.27 \ln (x) - 86.27 \ (DF = 38, \ r^2 = 0.77, \ P < 0.001)$$
(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 (Gjosaeter and Kawaguchi 1980).
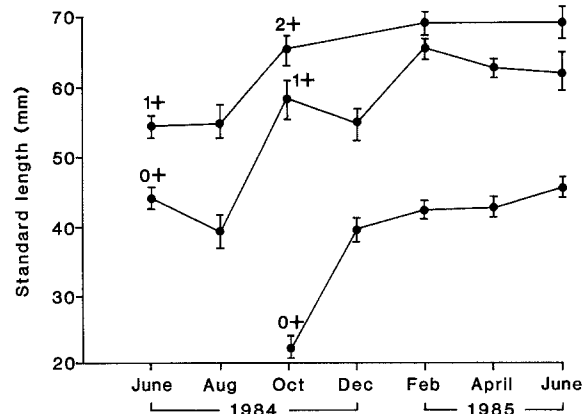

Fig. 5. *Lampanyctodes hectoris*. Growth rates of age classes derived from otolith analysis (± 2 SE)
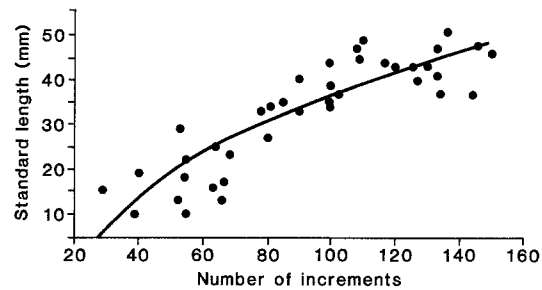

Fig. 6. *Lampanyctodes hectoris*. Relationship between standard length and number of increments in juvenile fish
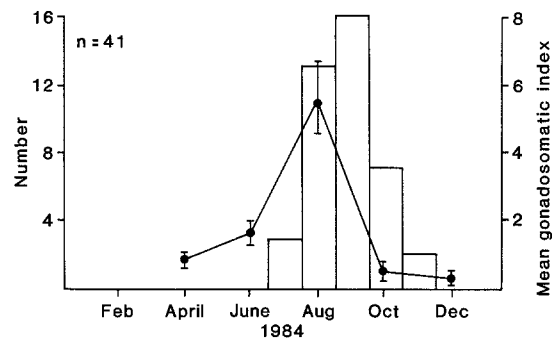

Fig. 7. *Lampanyctodes hectoris*. Back-calculated birthdates of Age 0+ fish estimated from daily increments (histogram). Right-hand axis refers to mean gonadosomatic indices ($\pm 95\%$ confidence limits) of mature females for same period (data from Young et al. 1987)

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 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.
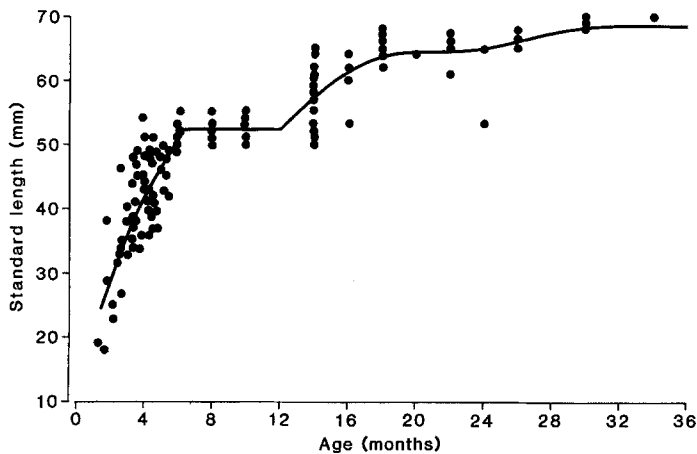
Fig. 8. *Lampanyctodes hectoris*. Growth curve from daily increments and annual data
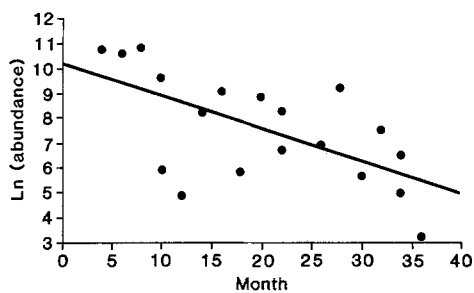
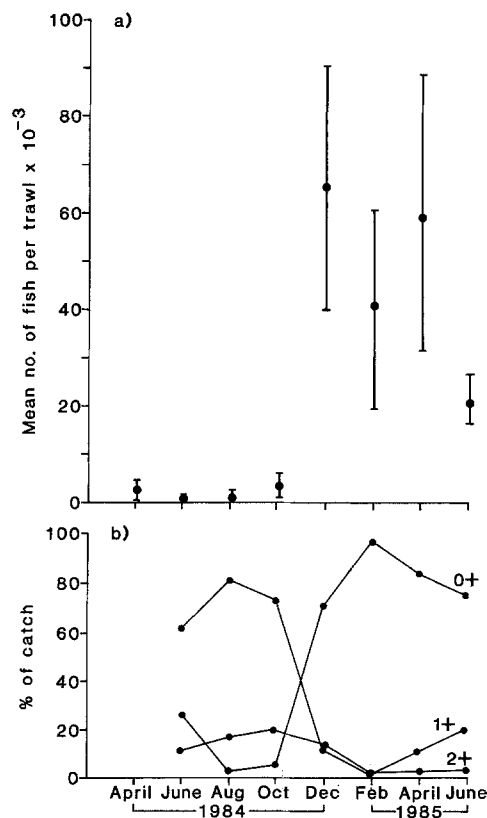**Fig. 9.** *Lampanyctodes hectoris*. Relative abundance of each age class versus age in months

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

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

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

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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