

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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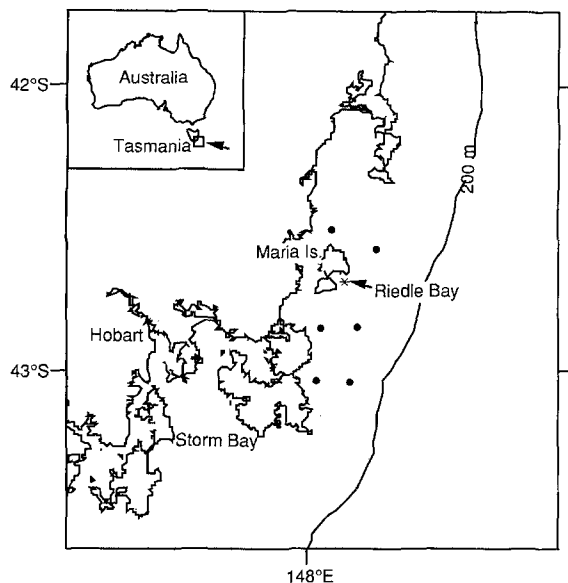


Fig. 1. Location of sampling stations (●) for *Nyctiphanes australis* around eastern Tasmania

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:

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

where P_s is the numerical proportion of a size class in the sample, N_s 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).

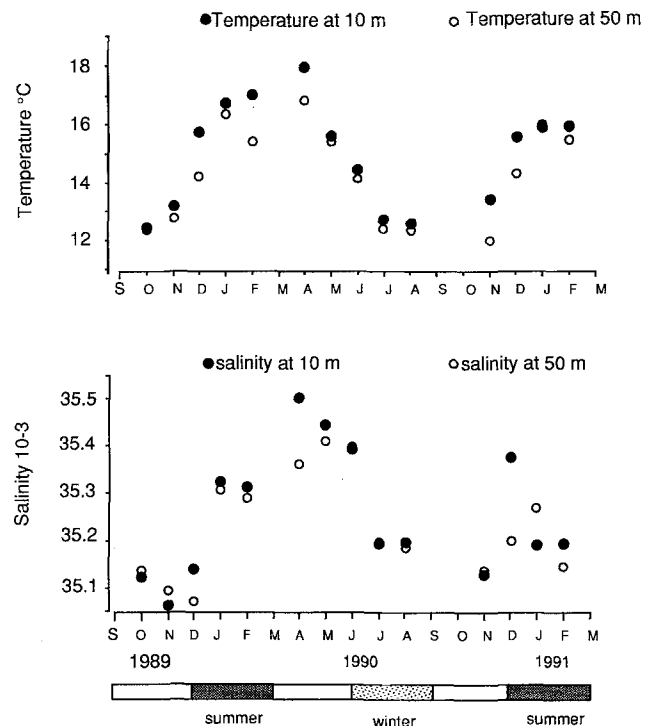
Interannual differences in *Nyctiphanes australis* biomass were compared by ANOVA on the coarse-scale data. Selection for prey size was examined using Pearre's C-index (Eq. 3, p. 915 in Pearre 1982). Each size class of *N. australis* was treated as an individual taxon and its proportion in the environment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

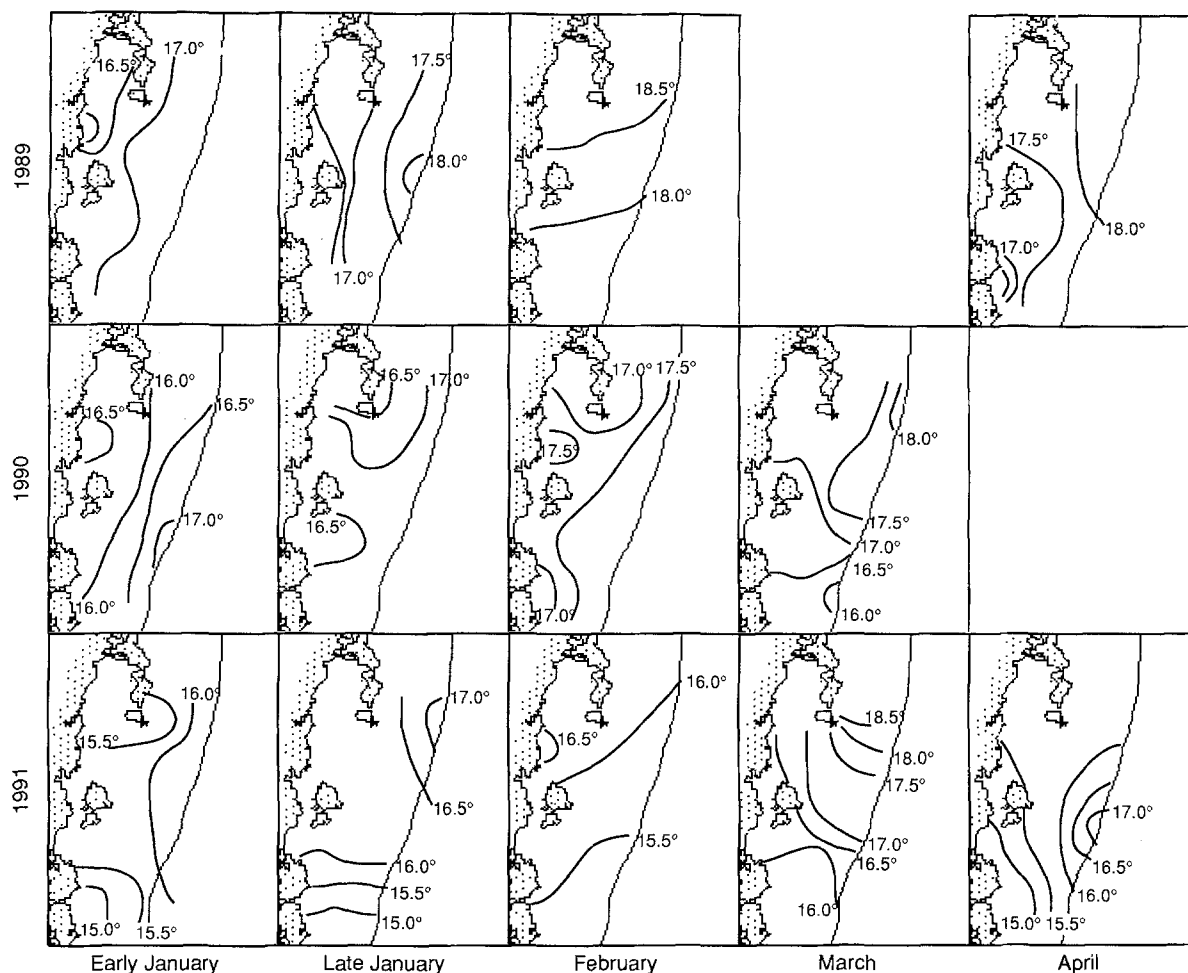


Fig. 3. Distribution of sea-surface temperatures ($^{\circ}\text{C}$) in shelf waters of eastern Tasmania during summer and autumn of 1989, 1990 and 1991

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

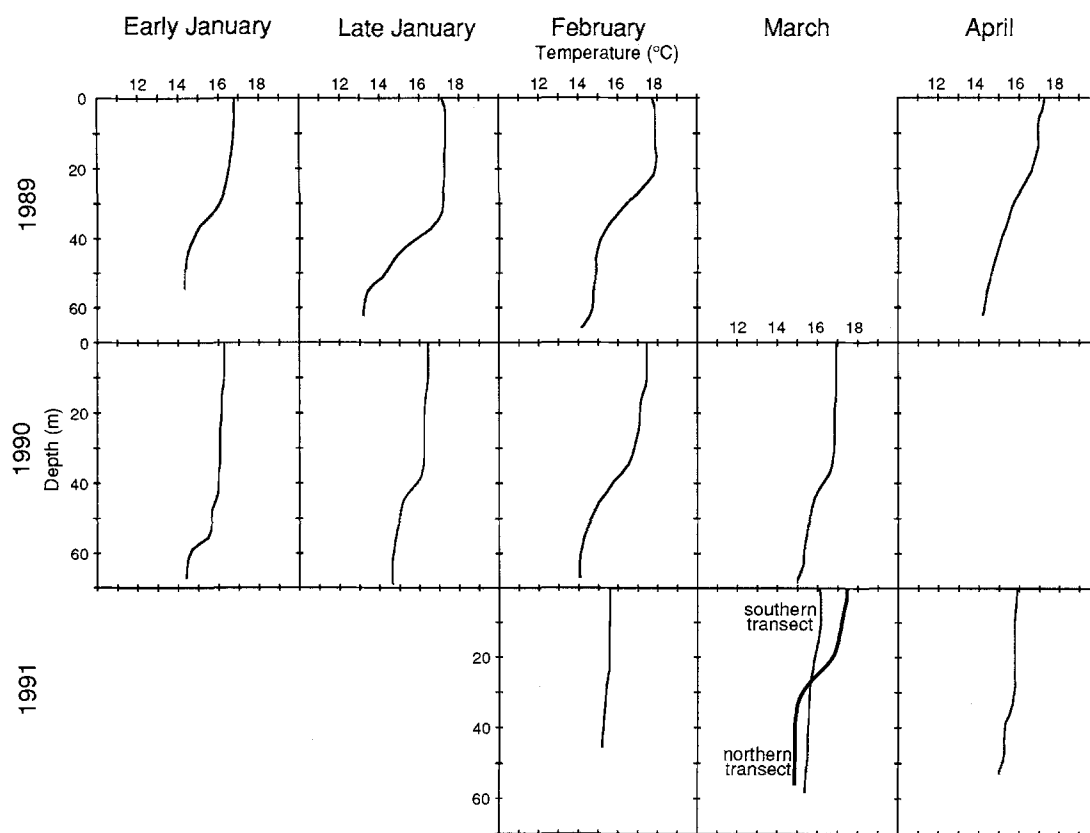


Fig. 4. Vertical temperature profiles at midshelf station immediately south of Maria Island during summer and autumn of 1989, 1990 and 1991. For March 1991, profile from midshelf station north of Maria Island is also presented (heavy line)

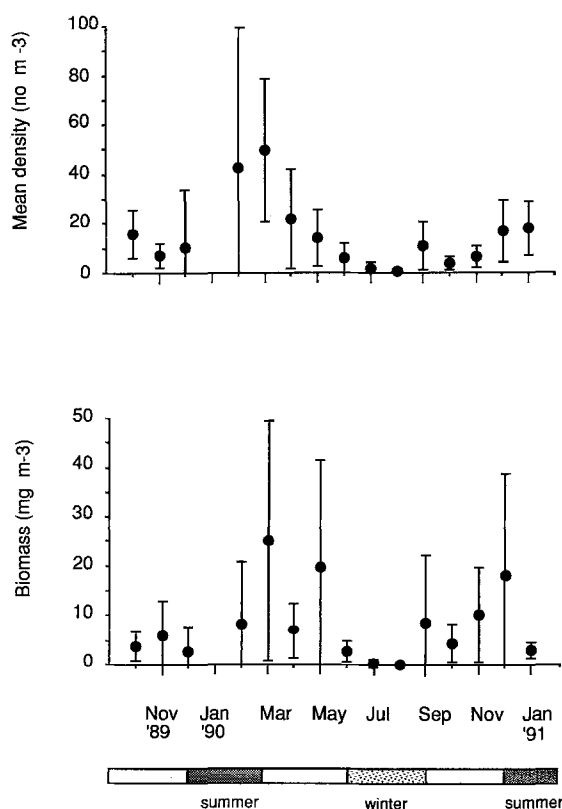


Fig. 5. *Nyctiphanes australis*. Monthly density and biomass at Riedle Bay (means $\pm$ 95% confidence limits)

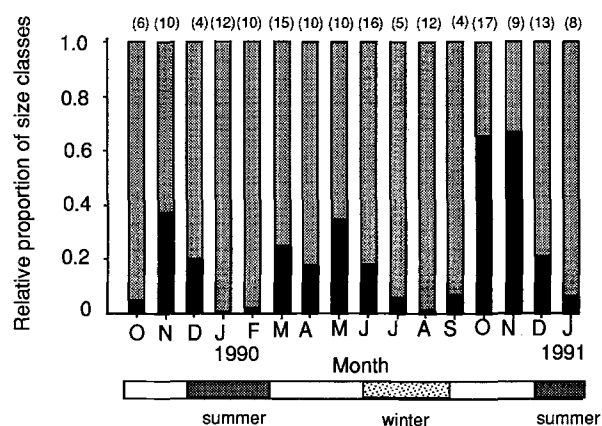


Fig. 6. *Nyctiphanes australis*. Relative proportions of size classes between months at Riedle Bay. Stippled portions represent Size Classes I and II combined, black portions represent Size Classes III and IV combined. Nos. in parentheses on top abscissa indicate number of samples

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

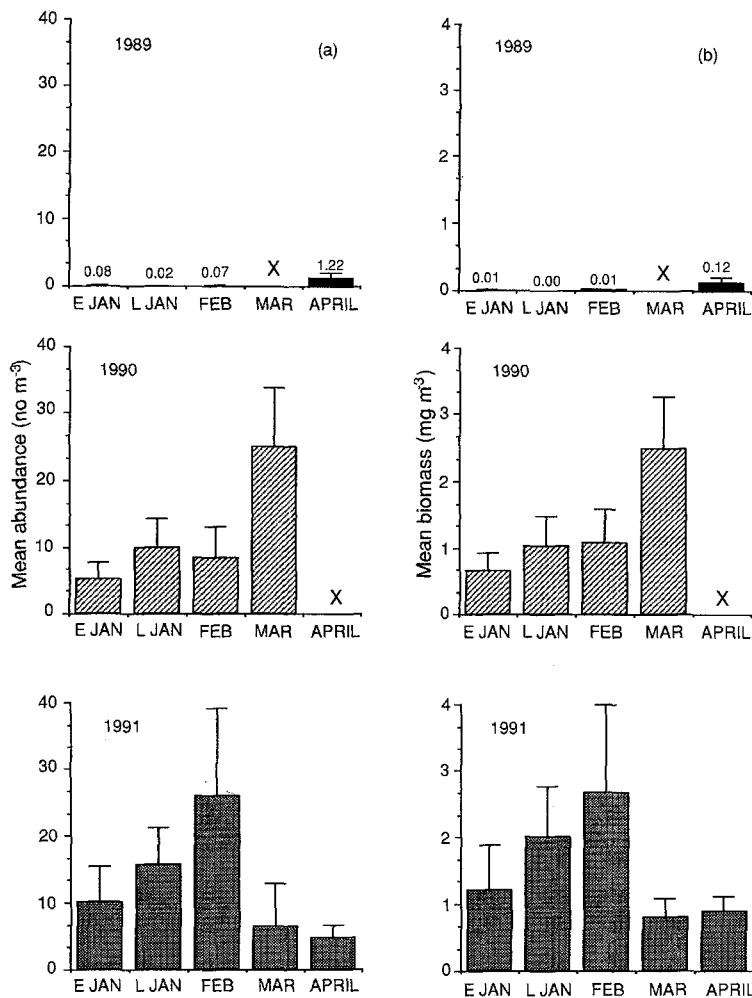


Fig. 7. *Nyctiphanes australis*. Interannual changes in density and biomass recorded during coarse-scale sampling off eastern Tasmania in 1989, 1990 and 1991 (means $\pm$ 1 SE; $n=6$ for all samples). E JAN, L JAN: early and late January respectively; X: no sampling

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 ($F=1.92$, $df=8, 82$, $p>0.05$).

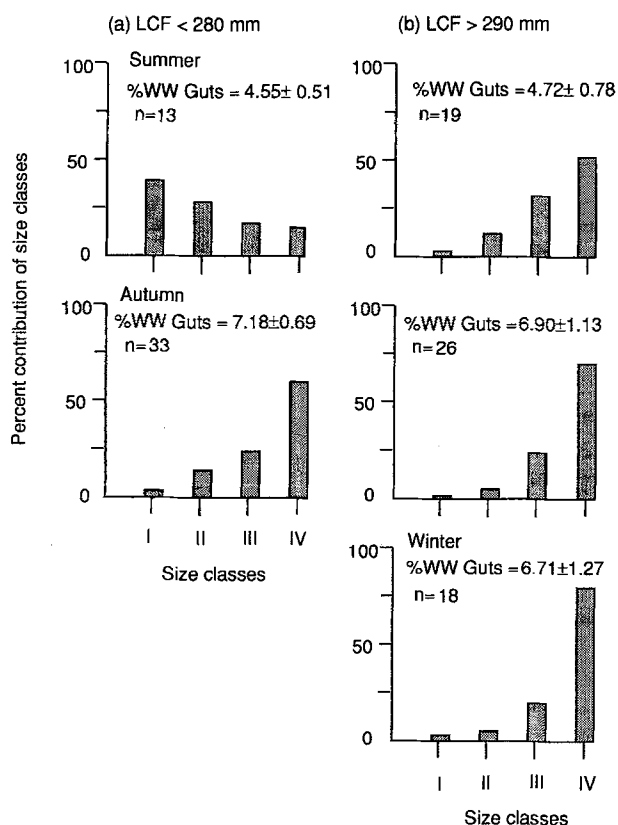
At night there was no significant difference in size distributions between surface and oblique tows ($F=0.17$, $df=6, 52$, $p>0.05$). We therefore combined data from both sets of tows and found that at night there was a significant difference in size distributions between seasons ($F=3.30$, $df=10, 60$, $p>0.01$). 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 $0.38 \text{ individuals m}^{-3}$) 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

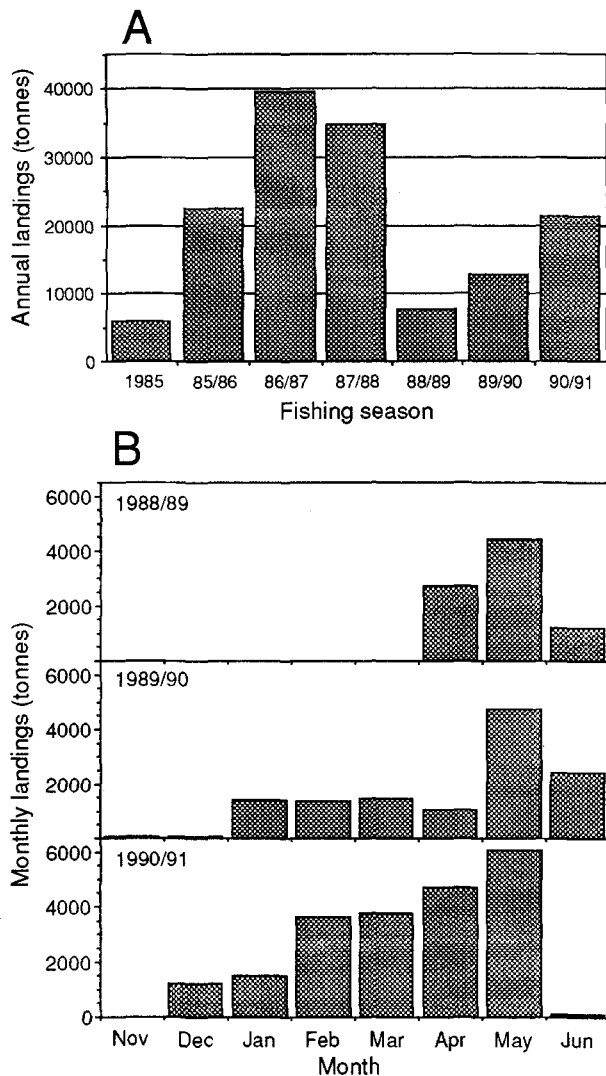


Fig. 9. *Trachurus declivis*. Annual fishery landings between 1985 and 1991 (A) and monthly fishery landings (B) during study period

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. 9A) 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. 9B). 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. 9A).

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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