Variability in thermocline depth and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters

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ABSTRACT: In this paper the dynamic nature of thermoclines is documented, and their influences on the vertical distributions of larval fishes and mesozooplankton in coastal waters off Sydney, southeastern Australia are tested. Significant small-scale spatial and temporal variability in thermocline depth and strength was observed, and even though there were strong depth-related differences in abundances of fish larvae and mesozooplankton, there were no predictable effects of thermoclines on their vertical distributions. Peak concentrations of some fish larvae were observed in thermoclines, but these patterns were not consistent among sampling locations and time periods. Fish larvae and mesozooplankton were most concentrated in the upper 30 m of the water column, regardless of thermocline position, and therefore trophic interactions among fish larvae and zooplankton would be strongest in this depth strata. Consequently, thermoclines were not considered the most important interface for trophic interactions in this dynamic coastal zone. We argue that thermoclines are probably not critical to the survival of fish larvae in relatively shallow coastal waters characterised by dynamic oceanographies where perturbations in the position and intensity of thermoclines are frequent.

KEY WORDS: Ichthyoplankton · Zooplankton · Oceanography · Thermocline stability and persistence · Vertical distribution · Southeastern Australia

INTRODUCTION

Larval fishes display a vast array of vertical distributions, and by way of their complex behaviours they may actively alter their vertical distributions in response to the interactive effects of various biotic and abiotic features of their environment (Leis 1991a, Heath 1992). Maintenance and regulation of vertical distribution can aid survival and affect dispersal during the early pelagic phase (Norcross & Shaw 1984, Cowen et al. 1993). Knowledge of interactions among fish larvae and the biotic and abiotic components of the pelagic environment is important for a greater understanding of recruitment processes as well as the overall dynamics of fish populations.

Oceanography has been argued to be able to explain the vertical distributions of larval fishes and zooplankton in the open ocean where gradients of temperature, salinity and light, and features such as thermoclines and haloclines are often persistent in space and time (Kendall & Naplin 1981, Perry & Neilson 1988, Frank et al. 1989, Munk et al. 1989, Röpke et al. 1993). Vertical distributions of fish larvae have often been related to that of their prey (Fortier & Leggett 1984, Munk et al. 1989) and predators (Brewer et al. 1984, Bailey & Houde 1989), and fish larvae and zooplankton have often been found to be concentrated in thermoclines (Haney 1988, Harris 1988, Heath et al. 1988, Frank et al. 1989). Thermoclines are, therefore, considered an important interface for trophic dynamics and the sta-

bility and persistence of such features has been hypothesised to be important to the survival of some larvae and may even influence year class strength (Lasker 1975, 1981). In contrast to the open ocean, thermoclines and haloclines can be highly dynamic in nearshore environments. For example, the nature of pycnoclines in nearshore waters may vary according to: (1) perturbations of the thermocline caused by internal waves that may be of high amplitude (e.g. 20 m, Middleton et al. 1996) and move at appreciable velocities (e.g. 0.25 to 1.25 km h^{-1}, Kingsford & Choat 1986); and (2) rapid changes in thermocline position due to changes in mainstream currents and eddies, wind-driven upwelling and downwelling, and storm events (Huyer et al. 1988, Griffin & Middleton 1991, Middleton et al. 1996). The responses of fish larvae and zooplankton to a variable, vertically stratified environment is largely unknown.

Previously, Gray (1996) showed that thermocline position and intensity did not predict the vertical distributions of larval fishes in shelf waters adjacent to Sydney. In this study, we expand on the findings and arguments of Gray (1996) by analysing a more comprehensive data set that includes vertical distribution information of mesozooplankton. Specifically we: (1) document the variable nature of thermoclines in the coastal waters off Sydney; (2) test relationships between thermoclines and vertical distributions of fish larvae and mesozooplankton; (3) assess relationships between selected fish larvae and mesozooplankton during the day and night; and (4) identify the most important depth strata for trophic interactions between fish larvae and zooplankton in these waters. We examine a suite of the most common fish larvae and assess relationships with specific mesozooplankton, including prey (cladocerans) and potential predators/competitors (copepods, chaetognaths and salps) (Zeldis et al. 1995, Baier & Purcell 1997). We discuss our findings in relation to current theories concerning the importance of physical and biological structure to plankton vertical distributions, and present arguments which suggest that trophic links in this community would be greatest in shallow strata, regardless of thermocline position, and that thermoclines may not be critical to the survival of fish larvae in coastal waters characterised by dynamic oceanographies.

MATERIALS AND METHODS

Oceanography and thermal stratification of the coastal waters off Sydney. The coastal waters off Sydney (Fig. 1) are characterised by a dynamic oceanographic regime, which is influenced by the East Australian Current and associated eddies, coastal-trapped waves, and local wind forcing (Freeland et al. 1986, Huyer et al. 1988, Middleton et al. 1996). The water column is usually thermally stratified between September and May (spring to autumn), with stratification usually greatest in January to April when differences in water temperature between surface and bottom (50 m) waters can exceed 5°C (Hahn et al. 1977). Between June and August (winter), the water column is generally well mixed, when differences in water temperatures between surface and bottom can be as little as 0.5°C. The depth and strength of the thermocline on the Sydney shelf can vary greatly over short time scales (e.g. hourly), and between relatively close locations along and across the shelf (Cox 1992, 1993, Middleton et al. 1996).

Sampling procedures. Day-time sampling of larval fishes, zooplankton and the temperature and salinity characteristics of the water column was undertaken in February and October 1991, and February, September and November 1992. In each period, sampling was done at 4 locations; North Head, Malabar, Port Hacking and Marley, where water depth ranged between
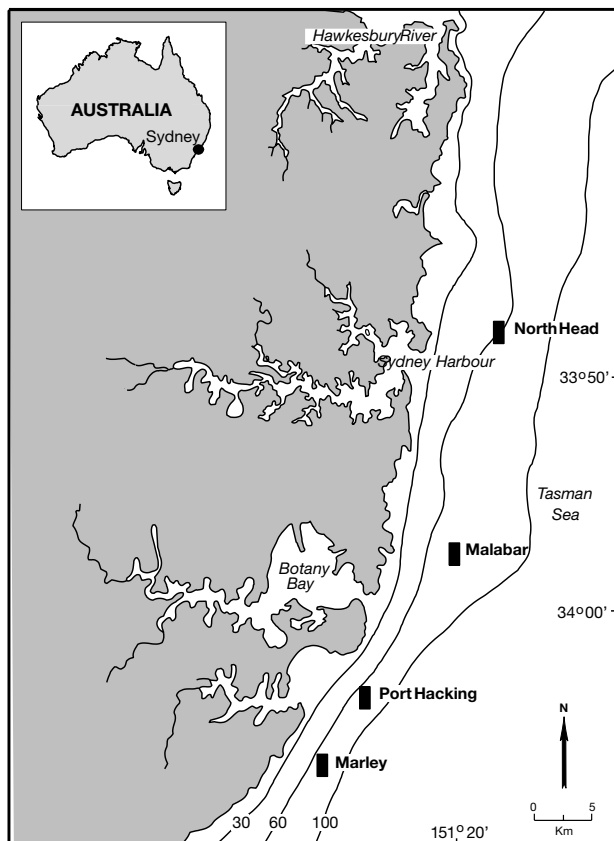

Fig. 1. Map of the study area showing the positions of the North Head, Malabar, Port Hacking and Marley sampling locations

60 to 80 m (Fig. 1). The different sampling periods were chosen based on times that the physical structure of the water column was likely to differ (i.e. stratified/unstratified). At Port Hacking and Marley sampling was also performed during the day and night in May and June 1993 to examine diel changes in vertical distributions and associations between fish larvae and zooplankton.

During the longer-term daytime component of the study, fish larvae and zooplankton were sampled at specific depths, nominally the surface (= 0 m), 5, 15, 30, 45, 55 and 65 m, whereas during the diel component of the study, samples were taken at 0, 10, 30 and 50 m. These intervals of sampling were chosen to allow sampling above, within and below thermoclines, based on previous knowledge of the thermocline structure. Cylindrical/conical nets with 80 cm diameter mouth, 500 μm mesh in the body and 250 μm mesh in the collecting bag, and fitted with open-close mechanisms (General Oceanics model DT-1000) to prevent contamination of samples during net deployment and retrieval, were used in all sampling (see Gray 1996). Three replicate 5 min horizontal tows were done at each depth at each location. The order in which replicate samples were taken at each depth was chosen randomly and it took approx. 4 h to complete sampling at each location. A flow meter positioned in the mouth of each net measured the amount of water filtered during each tow. During the first 2 daytime sampling periods, no samples were collected at the surface or at 65 m. At North Head, no 65 m samples were collected as total water depth was 60 m. Each location was sampled on a different day during each daytime period, and when possible the 4 locations were sampled on consecutive days, except when bad weather and/or prior commitments of the research vessel restricted sampling. During the diel component of the study, both Port Hacking and Marley were sampled on the same day and night. All fish larvae and zooplankton collected in each replicate haul were immediately preserved in 5% formaldehyde/seawater.

Temperature and salinity profiles of the water column at each location in each sampling period were determined by lowering and retrieving a submersible data logger (SDL—Yeokal model 6060) twice at each location, usually before and after the biological sampling. Descent speed of the SDL was < 0.2 m s^{-1}. These data were used to compare patterns of vertical distribution of fish larvae and mesozooplankton with the physical structure of the water column.
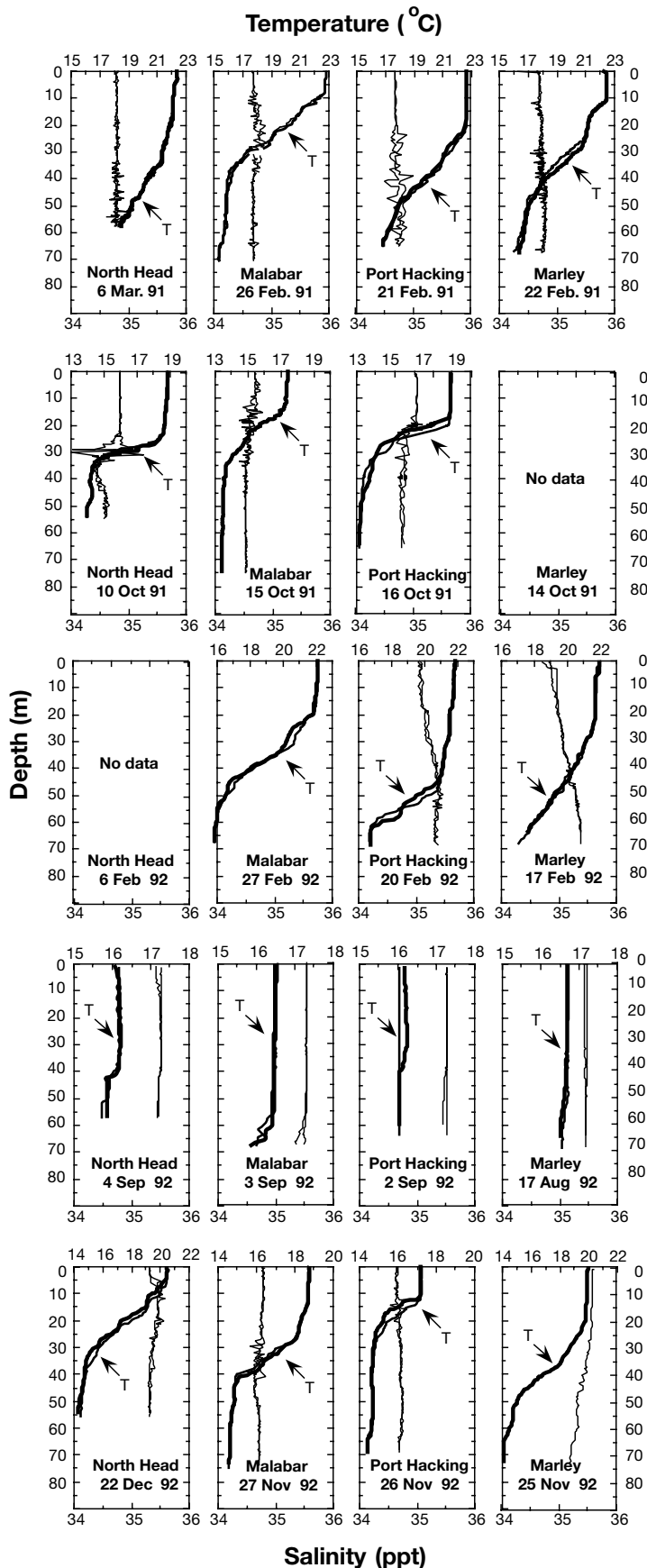
Laboratory procedures. Laboratory procedures followed those detailed in Gray (1993, 1996). All fish larvae were sorted from catches, identified, counted and their developmental stage determined under a binocular microscope. Fish were grouped for analytical pur-

poses as preflexion (pre- and flexion fish) and postflexion (postflexion and juvenile fish). Yolk sac larvae were not included in the analyses because of the large mesh size used in the net.

A suite of the most common fish larvae and their relationships with *Penilia avirostris*, copepods, chaetognaths and salps were examined for Port Hacking and Marley in February 1991 and 1992, and for the day and night samples in May and June 1993. Concentrations of mesozooplankton were determined by subsampling (n = 3 × 200 ml) the total catch of each replicate tow. Each invertebrate taxa was counted under a binocular microscope.

Treatment and analyses of data. Numbers of fish larvae caught in each replicate tow were standardised to the number per 100 m^3 of water, whereas zooplankton catches were standardised to number per 1 m^3 of water. Correlation analyses (Spearman rank correlation coefficient) were used to assess relationships between: (1) the thermal structure of the water column, i.e. the degree of change in water temperature between depths (0, 5, 15, 30, 45, 55, 65 m) and concentrations of fish larvae and mesozooplankton; and (2) concentrations of fish larvae and mesozooplankton among depths. Correlations were done separately for each location and sampling period, primarily because thermoclines varied at that scale. We acknowledge that each individual correlation was relatively weak (maximum degrees of freedom = 18) and with many correlations there is an increased chance of Type I errors (i.e rejection of the null hypothesis by chance alone) occurring. However, because we primarily used the correlation analyses to seek patterns, we chose not to use the Bonferroni correction factor (i.e. 0.5 n^{-1}) to correct for Type I errors as it would have made the analyses extremely conservative (less powerful), thus increasing the associated risk of Type II error (acceptance of the null hypothesis by chance alone—a serious concern given that many of our analyses were nonsignificant, see 'Results'). Alpha in each individual test was therefore not reduced below the convention of 0.05. Our assessment was based on the expectation that 1 in 20 correlations (i.e. 5%) may have been significant by chance alone. When the number of significant correlations for any particular period was < 5%, it was concluded they may have been by chance alone and thus they were ignored. Likewise, if more than 1 in 20 correlations (i.e. > 5%) for any particular period were significant, it was most likely that these were not by chance alone, and thus they were accepted.

To examine our data in a more powerful way, to account for Type II errors and to test the consistency of results across locations within each period and across periods, we further analysed the independent probabilities obtained from the original rank correlations in a

Fig. 2. Temperature and salinity profiles of the water column at each study location on each day of sampling in the 5 daytime sampling periods. Two replicate profiles are shown for each location except Marley in November 1992. T = temperature profile

series of meta-analyses (Fisher's combined log probabilities test—Fisher 1935). The procedure for doing these meta-analyses followed that outlined in Underwood (1997). We also note that visual assessments of the data were used in conjunction with the correlation and meta-analyses to describe the patterns observed.

RESULTS

Variability in thermocline depth and intensity

The water column was thermally stratified in all daytime sampling periods except September 1992 (Fig. 2). The depth and intensity of thermoclines varied greatly among locations, within and between sampling periods. Sharp discrete thermoclines were evident at North Head and Port Hacking in October 1991, Port Hacking in February 1992 and at Malabar and Port Hacking in November 1992, whereas thermoclines were generally more gradual at other times, some extending >20 m (e.g. Port Hacking and Marley in February 1991, Malabar and Marley in February 1992, Marley in November 1992) (Fig. 2). Depth of water at the top of the thermocline (>0.5°C change in temperature in 1 m depth interval) varied from 10 m (e.g. Malabar and Marley in February 1991) to 50 m (e.g. Port Hacking in February 1992). Salinity usually fluctuated around the thermocline, but there was no evidence of any distinct halocline at any location (Fig. 2).

In May and June 1993 there was no thermal stratification at either location, day or night. In May surface water was 19.4°C and at 65 m it was 19.2°C, whereas in June surface and bottom water was 18.1°C.

Relationships between thermoclines and larval fishes

Strong depth-related differences in numbers of total taxa, pre- and post-flexion larvae were evident, although there were no consistent relationships with thermocline position (Fig. 3,

Table 1). Greatest larval diversity and abundance was usually found from 10 to 30 m, regardless of oceanographic conditions. For example, numbers of total taxa and pre-flexion fishes displayed significant positive correlations with change in water temperature in October 1991 and November 1992, but significant negative correlations in February 1992 (Table 1). In the absence of a thermocline in September 1992, the numbers of total taxa, pre- and post-flexion larvae displayed patterns of depth distribution that were similar to those when thermoclines were present in other sampling periods (Fig. 3). Most fish larvae caught were preflexion, and this was evident across all depths and locations in all sampling periods (Fig. 3).

There were no predictable effects of thermoclines on vertical distributions of all fish taxa, as relationships varied among taxa, locations and sampling periods— significant positive and negative relationships were
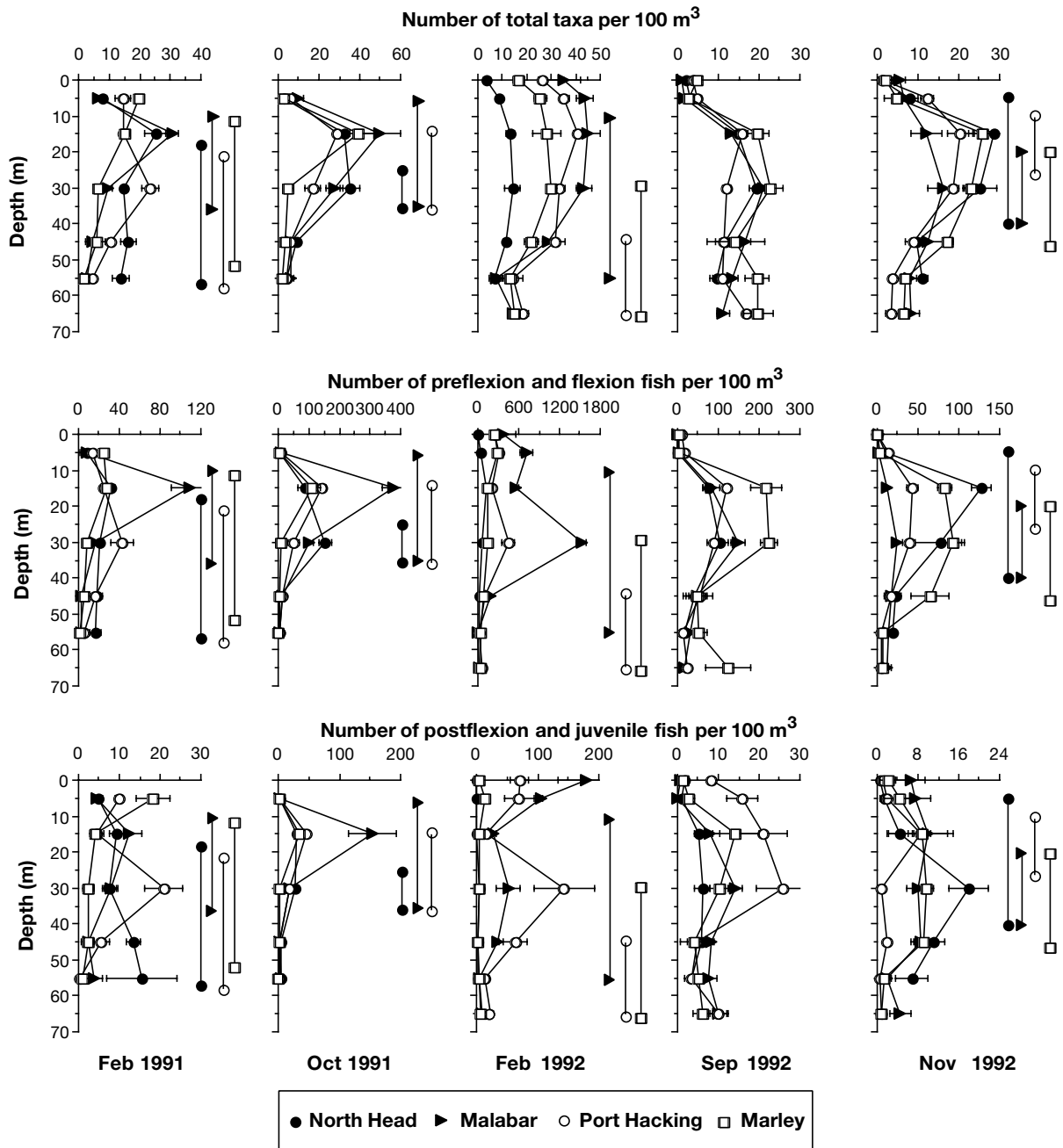

Fig. 3. Vertical distributions of total taxa, pre- and postflexion fishes and position of thermocline in each sampling period. Vertical lines on right show thermocline position at each location. No thermocline was present in September 1992

Table 1. Summary of results of Spearman rank correlation analyses between concentrations of fish larvae and incremental change in water temperature with depth at each of the 4 locations in the 4 sampling periods that thermoclines were present, and significance of Fisher combined log probability tests. +: significant positive correlation at p < 0.05; –: significant negative correlation at p < 0.05; ns: correlation not significant at p > 0.05; (degrees of freedom for each correlation: 13 in February and October 1991, 18 in February and September 1992); NH: North Head; MR: Malabar; PH: Port Hacking; MY: Marley. Note that no temperature data was available for Marley in October 1991 and North Head in February 1992 and there was no thermocline present in September 1992. Vertical distributions of selected fish larvae are shown in Figs. 3 to 6

| | February 1991 | | | | October 1991 | | | February 1992 | | | November 1992 | | | |
	NH	MR	PH	MY	NH	MR	PH	MR	PH	MY	NH	MR	PH	MY
Total taxa	ns	+	ns	ns	ns	+	+	ns	–	–	+	+	+	+
Preflexion fish	ns	+	ns	ns	+	+	+	ns	–	–	+	+	+	+
Postflexion fish	ns	ns	ns	ns	ns	+	+	ns	ns	ns	+	ns	ns	+
No. of correlations	9	9	9	9	15	15	15	30	30	30	15	15	15	15
No. of significant +	1	4	2	0	3	11	13	6	3	1	10	5	9	11
No. of significant –	1	1	0	2	0	0	0	8	7	6	0	0	0	0
Fisher test (P)	>0.05	<0.01	<0.01	>0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

observed (Table 1, Figs. 4 to 6). Several taxa (e.g. *Gerres subfasciatus*, *Gonorynchus greyi*, *Kyphosus* sp., Pomacentridae) that displayed significant negative relationships were restricted in their depth to the surface and 5 m. At Malabar in February 1991, Malabar and Port Hacking in October 1991 and at all 4 locations in November 1992, the vertical distributions of several taxa (including *Sillago flindersi*, *Cepola australis*, *Pseudocaranx dentex*, triglids and labrids) displayed significant positive correlations to change in water temperature. This generally coincided where thermoclines were relatively sharp and occurred at 20 to 40 m depth. Because there was a large number of significant correlations in these periods, we did not consider them to be caused by chance alone, and this was also confirmed by the Fisher combined log probability tests.

Although in total there were few significant correlations in most sampling periods, the Fisher combined log probability tests indicated that overall, there were significant relationships between fish larvae and water column thermal structure at all locations in all 4 periods examined, except North Head and Marley in February 1991 (Table 1).

Peak concentrations of some fish larvae coincided with thermocline position at some locations in each period. For example, in February 1991 *Trachurus* sp., bothids and triglids were most prevalent at 15 m at Malabar and Marley, but at 30 m at Port Hacking, which coincided with the shallowest depth sampled in the thermocline at each location (Figs. 4 to 6). These thermoclines were gradual, generally extending over 20 m. In October 1991 when thermoclines were generally shallow and sharp, *Sillago flindersi*, *Pseudocaranx dentex*, *Sardinops sagax*, bothids, triglids and labrids were most concentrated in thermoclines at 30 m at North Head and 15 m at Malabar, whereas, *Sardinops sagax*, triglids and labrids also displayed peak abun-

dance at 15 m at Port Hacking. In February 1992 *Pseudocaranx dentex*, bothids, platycephalids, triglids and labrids displayed peak abundance in a depth strata near the top of the thermocline at Malabar (15 to 30 m), but no such patterns were evident for these taxa at Marley and Port Hacking where peak abundance occurred above the deeper (below 30 m) thermocline (note that no temperature data was available for North Head). In November 1992 peak concentrations of *S. sagax*, *Engraulis australis* and platycephalids occurred in the thermocline at 15 m at North Head, but not elsewhere (Figs. 4 to 6).

In the absence of a stratified water column in September 1992, several taxa displayed vertical distributions that were very similar to those in other periods when thermoclines were present. For example, *Pseudocaranx dentex*, *Sardinops sagax* and bothids were generally most abundant between 15 and 45 m (Figs. 4 to 6).

Relationships between thermoclines and mesozooplankton

Mesozooplankton vertical distribution appeared to be independent of water column stratification even though there were strong depth-related changes in their concentrations (Fig. 7, Table 2). It is noted, however, that during these sampling times thermoclines were generally broad, extending >15 m. Mesozooplankton were similarly distributed at both locations in both sampling periods even though thermocline depth and strength varied. Concentrations of all 4 taxa were greatest in the upper water column (<30 m) (Fig. 7), and there was a general trend for their distributions to be negatively correlated with change in water temperature (significant Fisher tests, Table 2). Peak concentrations of zooplankton occurred above thermoclines in

February 1992 and at Port Hacking in February 1991, whereas they generally peaked in the broad (10 to 50 m) thermocline at Marley in February 1991 (Fig. 7).

Relationships between larval fishes and mesozooplankton

There were few significant relationships between the concentrations of fish larvae and mesozooplankton (*Penilia avirostris*, copepods, chaetognaths and salps) at the Port Hacking or Marley locations in February 1991 or 1992 (Table 3), even though their vertical distributions generally overlapped. The Fisher tests sug-

gested there were some general associations between fish larvae and zooplankton, but these generally varied between locations and sampling periods—the notable exception being relationships with chaetognaths. Most significant relationships were positive: in February 1991 concentrations of bothids and eel leptocephali were positively related to *P. avirostris* across both locations, whereas *Trachurus* sp. and triglids were significantly correlated with *P. avirostris* at Marley. Similarly, total fish larvae taxa, pre-flexion larvae, *Trachurus* sp. and eel leptocephali were significantly related to chaetognaths at both locations in February 1991, as were bothids at Port Hacking, and triglids and gobies at Marley. In February 1992 *Centroberyx affinis* and
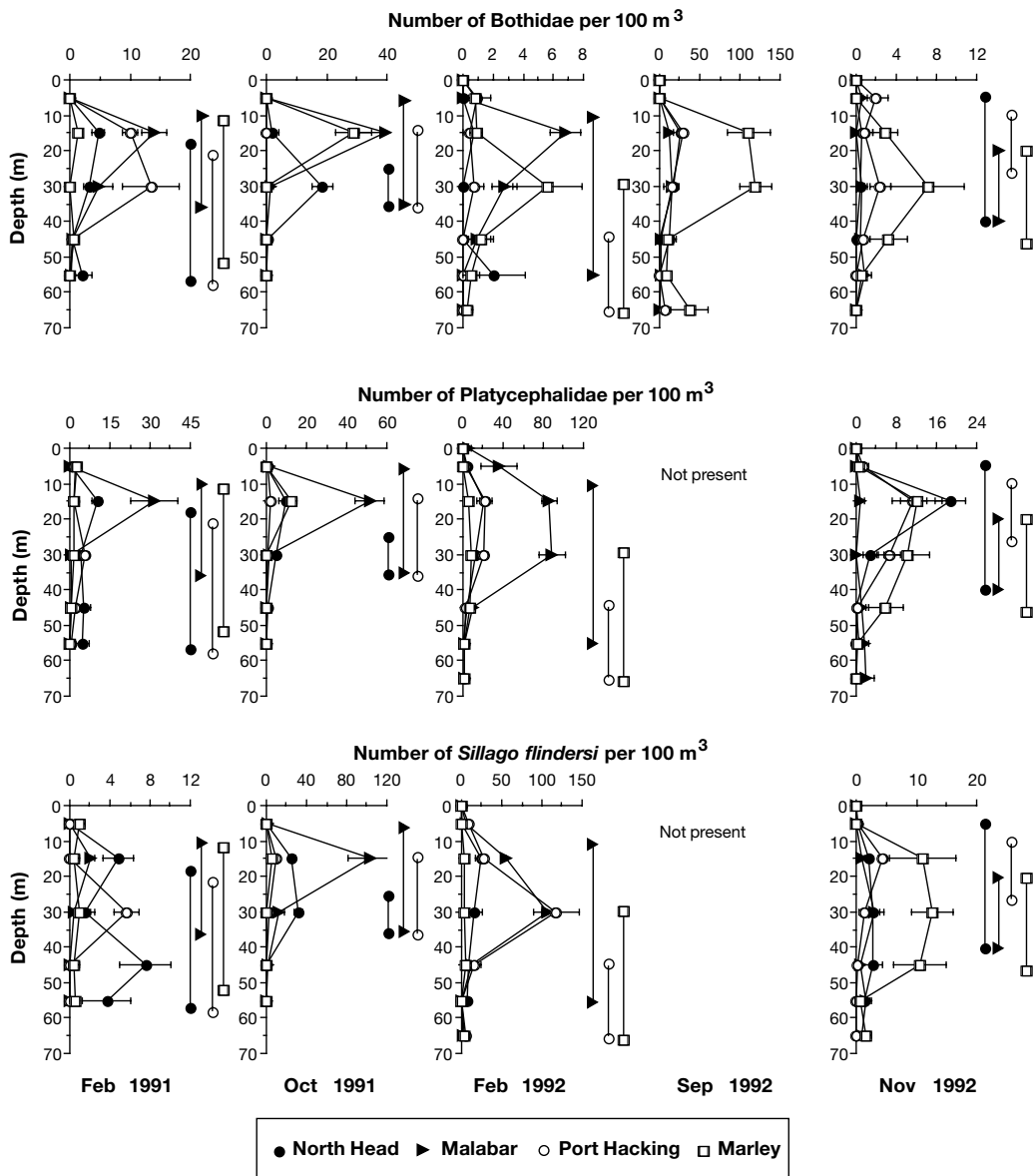

Fig. 4. Vertical distributions of Bothidae, Platycephalidae and *Sillago flindersi* and position of thermocline in each sampling period. Vertical lines on right show thermocline position at each location. No thermocline was present in September 1992
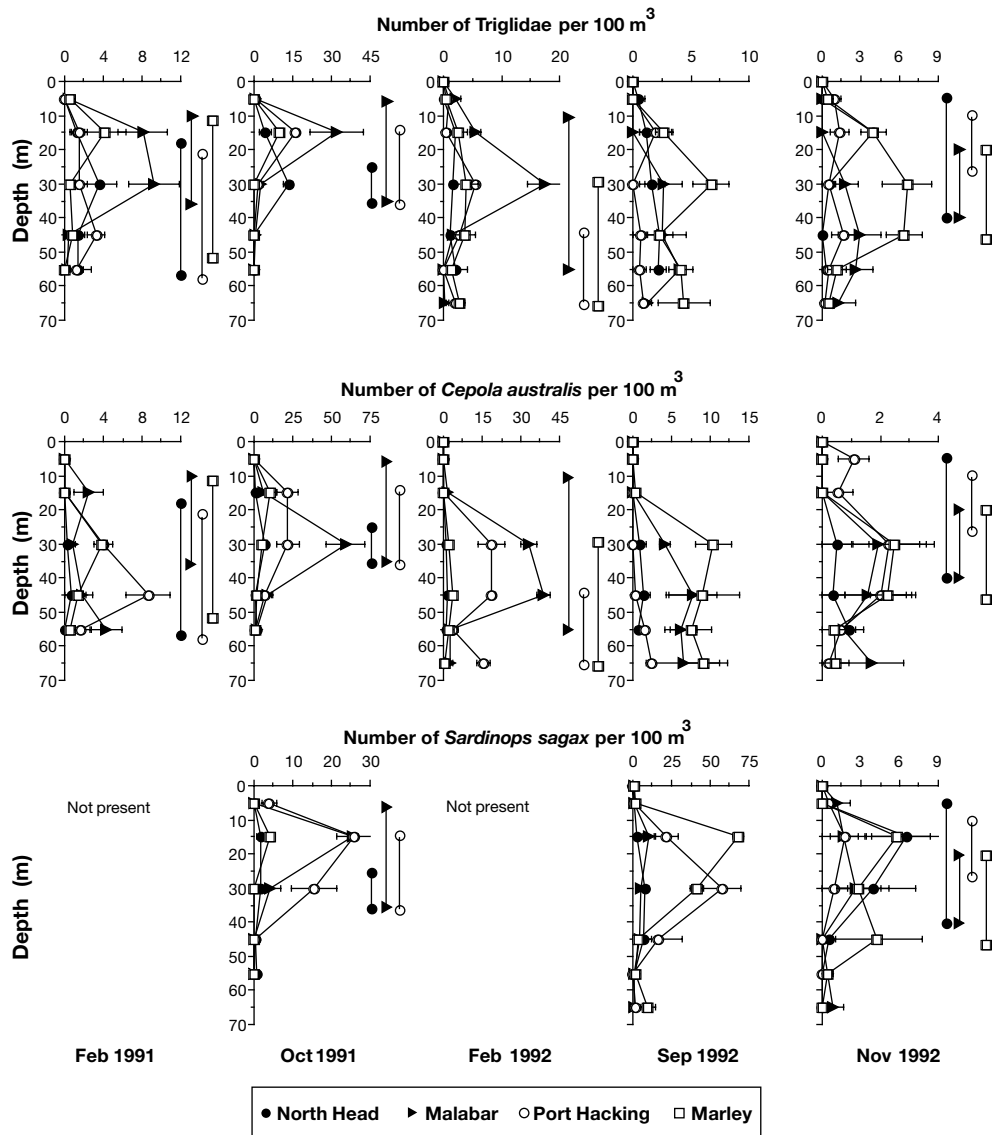
Fig. 5. Vertical distributions of Triglidae, *Cepola australis* and *Sardinops sagax* and position of thermocline in each sampling period. Vertical lines on right show thermocline position at each location. No thermocline was present in September 1992

pempherids were significantly related to *P. avirostris* and chaetognaths at both locations. These significant correlations may have been partly driven by the general preference for shallow water displayed by most taxa.

Diel changes in vertical distributions and relationships between larval fishes and mesozooplankton

Large day-night differences in vertical distributions of larval fishes were evident (Fig. 8). Greatest numbers of taxa occurred at 30 m during the day at both Port Hacking and Marley in May and June, whereas

similar numbers of taxa occurred across all depths at night (Fig. 8). Most larvae caught were preflexion, and this was evident across all depths at both locations, day and night (Fig. 8). In May, preflexion larvae were most abundant at 10 m both day and night at Port Hacking, whereas most occurred at 30 m during the day and at the surface at night at Marley. In June, greatest numbers of preflexion larvae were caught at the surface and least at 50 m during the day, but similar numbers tended to occur across all depths at night. Greatest numbers of postflexion larvae generally occurred at 10 and 30 m during the day in May and June, but again there were no clear patterns at night. Individual taxa also displayed distinct

depth distributions during the day, but these patterns broke down at night as most taxa became evenly dispersed throughout the entire water column (see Gray 1998).

Depth-related patterns in vertical distributions of the 4 zooplankton taxa tended to remain similar during the day and night at both locations in both sampling periods. *Penilia avirostris*, copepods and chaetognaths were generally most abundant at 10 and 30 m both day and night in May and June (Fig. 9). Copepods were also abundant at 50 m at Port Hacking during the day in June and at the surface at Port Hacking at night in May. Salps showed less obvious patterns, being more evenly distributed across all depths both day and night.

Few correlations (18.5%) revealed any significant relationships between concentrations of fish larvae and *Penilia avirostris*, copepods and chaetognaths (Table 4). Significant relationships varied among taxa, locations, day and night and between May and June.

DISCUSSION

Thermocline variability

We have documented the considerable variability in the characteristics of thermoclines over the inner continental shelf off Sydney. Although these waters are usually thermally stratified throughout spring to autumn, the dynamic oceanographic regime of the region means that the extent of thermal stratification is not predictable. Thermoclines can occur at any depth and may be weak or strong. Oceanographic events, such as the passage of internal and coastal-

Table 2. Results of Spearman rank correlation analyses between abundances of mesozooplankton and incremental change in water temperature with depth at Port Hacking and Marley in February 1991 and 1992 and significance of Fisher combined log probability tests. The correlation coefficient (*r*) for each correlation is shown (degrees of freedom = 13). *, **significant at p < 0.05, p < 0.01, respectively. Vertical distributions of mesozooplankton are shown in Fig. 7

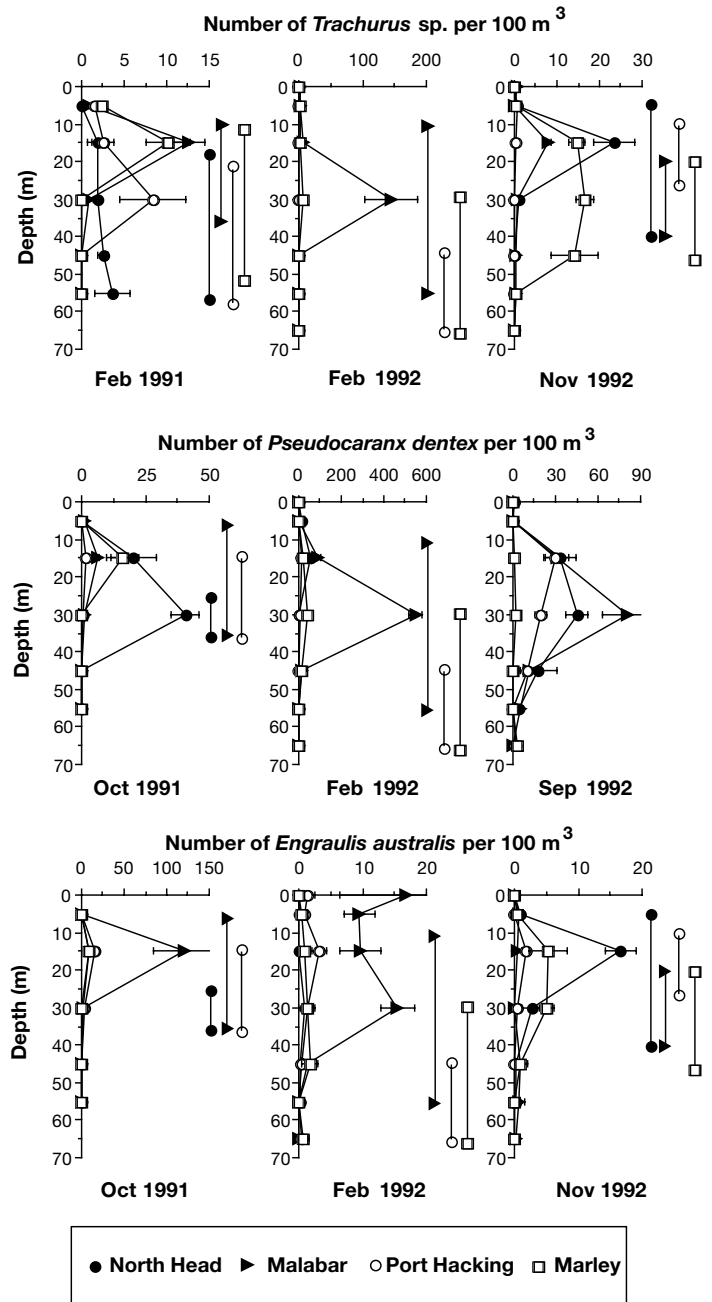| Taxon | February 1991 | | February 1992 | |
	Port Hacking	Marley	Port Hacking	Marley
Penilia avirostris	−0.426*	−0.164	−0.593*	−0.465
Copepoda	−0.599*	−0.065	−0.828**	−0.901**
Chaetognatha	−0.263	−0.322	−0.827**	−0.733**
Salpa	−0.364**	0.109	−0.672*	0.168
Fisher test (*P*)	<0.05	>0.05	<0.05	<0.05

Fig. 6. Vertical distributions of *Trachurus* sp., *Pseudocaranx dentex* and *Engraulis australis*, and position of thermocline in each sampling period. Vertical lines on right show thermocline position at each location. No thermocline was present in September 1992

trapped waves, advection of different water masses and storm events can dramatically alter the integrity of thermoclines, and therefore the depth and intensity of thermoclines can vary greatly between relatively close locations (5 to 20 km) along the continental shelf as documented here, as well as over short
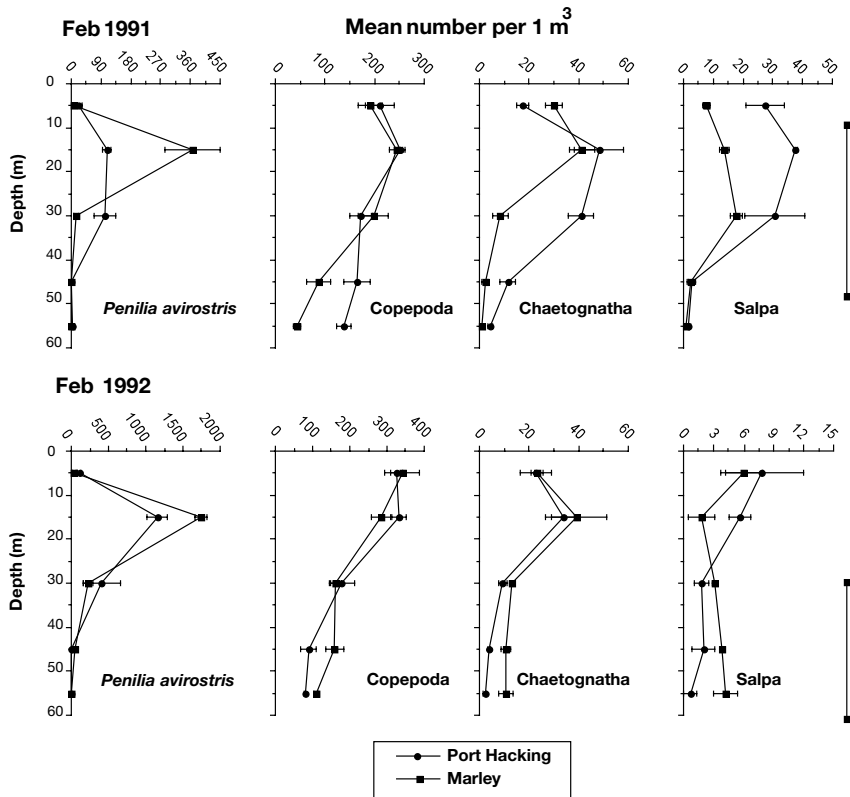
Fig. 7. Vertical distributions of mesozooplankton and position of thermocline at Port Hacking and Marley in February 1991 and 1992. Vertical lines on right show thermocline position at each location

(hours to days) time periods (see also Middleton et al. 1996, Lee & Pritchard 1997). The instability and lack of persistence of thermoclines in these waters may have profound effects on plankton distributions, particularly if there is a general preference for shallow water.

Variable thermoclines and plankton distributions

We provide evidence that thermoclines had no predictable effects on vertical distributions of larval fishes and mesozooplankton in the coastal waters off Sydney (see also Gray 1996). These conclusions were derived

Table 3. Summary of results of Spearman-rank correlation analyses between the concentrations of fish larvae and the concentrations of *Penilia avirostris*, Copepoda, Chaetognatha and Salpa across 5 depths at Port Hacking and Marley in February 1991 and 1992, and significance of Fisher combined log probability tests. Degrees of freedom = 13 for each correlation; PH = Port Hacking; MY = Marley

| | *Penilia avirostris* | | Copepoda | | Chaetognatha | | Salpa | |
	PH	MY	PH	MY	PH	MY	PH	MY
February 1991								
No. of correlations	10	10	10	10	10	10	10	10
No. of significant +	4	3	1	5	3	4	4	1
No. of significant –	0	0	0	0	0	0	0	0
Fisher test (P)	>0.05	>0.05	>0.05	<0.01	<0.05	<0.01	<0.05	>0.05
February 1992								
No. of correlations	20	20	20	20	20	20	20	20
No. of significant +	4	5	3	5	6	5	2	0
No. of significant –	0	0	1	1	0	2	0	0
Fisher test (P)	<0.05	<0.01	<0.01	<0.01	<0.01	<0.01	>0.05	>0.05
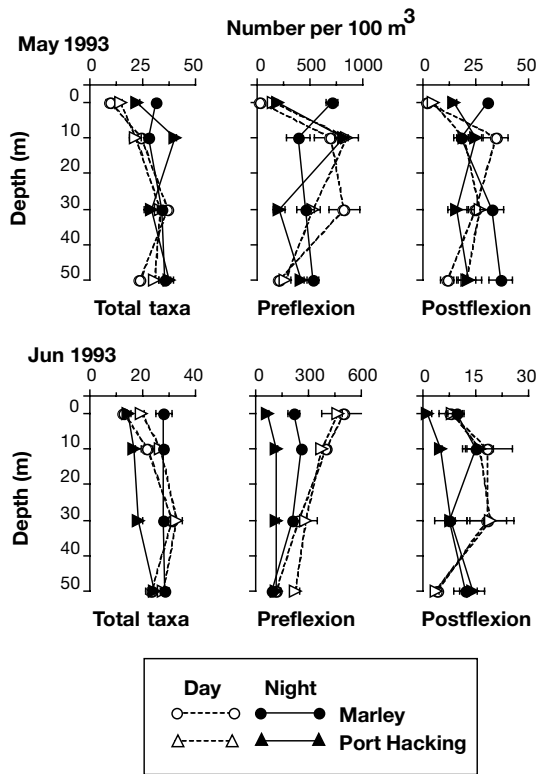
Fig. 8. Day and night vertical distributions of total taxa, pre- and postflexion fishes at Port Hacking and Marley in May and June 1993. No thermocline was present in either sampling period
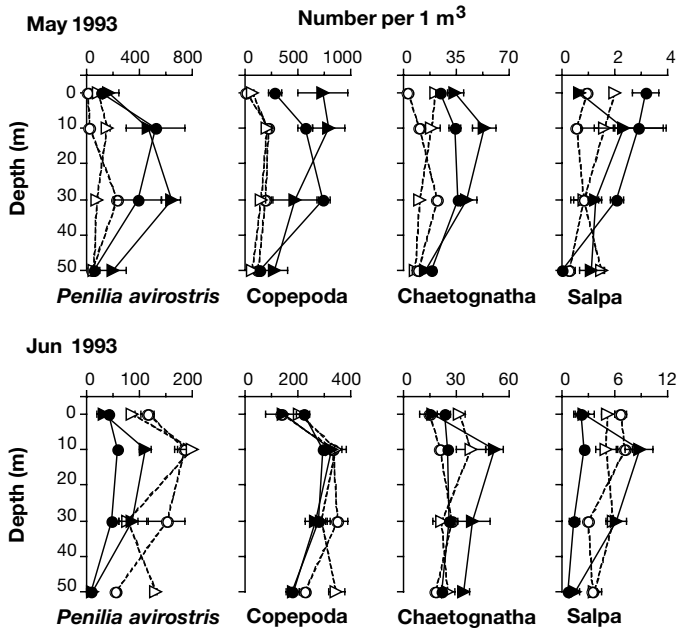

Fig. 9. Day and night vertical distributions of mesozooplankton at Port Hacking and Marley in May and June 1993. No thermocline was present in either sampling period. Symbols as per Fig. 8

by employing a stratified, quantitative and replicated sampling program that incorporated several depths, locations and time periods. We acknowledge that our results pertain only to organisms captured in 500 µm mesh, and thus may not be applicable to small yolk-sac larvae. Few researchers have tested relationships between thermoclines and fish larvae over a range of spatial and temporal scales as done here (but see Röpke 1993). Given that our results are in stark contrast to that generally presented for shelf and oceanic waters elsewhere (e.g. Kendall & Naplin 1981, Frost 1988, Haney 1988, Lough & Potter 1993), it is clear that paradigms concerning relationships between thermoclines and larval fishes and zooplankton are not universal (see also Röpke 1993).

Table 4. Summary of results of Spearman rank correlation analyses between concentrations of fish larvae and *Penilia avirostris*, Copepoda and Chaetognatha across 4 depths day and night at Port Hacking and Marley in May and June 1993, and significance of Fisher combined log probability tests. Degrees of freedom = 10 for each correlation; d: day; n: night

| | *Penilia avirostris* | | | | Copepoda | | | | Chaetognatha | | | |
| | Port Hacking | | Marley | | Port Hacking | | Marley | | Port Hacking | | Marley | |
	d	n	d	n	d	n	d	n	d	n	d	n
May 1993												
No. of correlations	20	20	20	20	20	20	20	20	20	20	20	20
No. of significant +	3	0	3	0	2	0	0	0	3	1	4	0
No. of significant −	0	0	0	3	0	0	0	4	5	0	0	5
Fisher test (*P*)	<0.01	>0.05	<0.01	<0.05	<0.05	>0.05	<0.05	<0.05	<0.01	>0.05	<0.01	<0.01
June 1993												
No. of correlations	20	20	20	20	20	20	20	20	20	20	20	20
No. of significant +	0	3	3	11	2	2	5	6	3	3	6	2
No. of significant −	0	2	2	0	1	2	0	0	0	1	2	0
Fisher test (*P*)	>0.05	<0.01	<0.01	<0.01	<0.01	<0.05	<0.01	<0.01	<0.05	<0.05	<0.01	<0.05

We argue that relationships between thermoclines and fish larvae were unpredictable because of the variable and dynamic nature of thermoclines in these waters. We suggest that plankters were unable to respond to thermocline changes in a time frame that permitted consistent relationships to be observed. Thermoclines may require stability and persist for some extended period for consistent relationships to be developed. Fish larvae and zooplankton may display a 'lag' in their response time to changes in thermocline depth and intensity. Consequently, in waters where thermoclines are being shunted up and down the water column at irregular intervals, there may be relatively few occasions when fish larvae display strong associations with thermoclines. This may explain why in some sample periods fish larvae were sometimes most abundant in thermoclines at some locations and not at others. The suggested lag in response time of fish larvae to thermocline change could be tested by more intensive (continual) sampling of the water column over a couple of days during stable and turbulent periods (e.g. presence/absence of internal waves). We further suggest that relative differences in the persistence of thermal stability of different waters may have strong impacts on associations between thermoclines and biota, and this may also explain some differences in the observations found here and in other waters. In waters where thermoclines are relatively stable over a given depth strata for some extended period of time, relationships between fish larvae, zooplankton and thermoclines may be more prominent. This, for example, could lead to fundamental differences in the ecology of plankton in waters of different oceanographic influence (e.g. open oceans versus nearshore waters).

Larval fishes and zooplankton may respond in different ways to sharp distinct thermoclines as opposed to gradual thermoclines, and similarly shallow as opposed to deep thermoclines. Most thermoclines in this study were gradual, extending 20 to 30 m of the total 70 m water depth, and this may have contributed to the general lack of observed relationships. Thermoclines may only be important when they are intense and occur over a small proportion of total water depth. Notably, several types of fish larvae were most concentrated in the sharp and relatively shallow (<30 m) thermoclines at Malabar and Port Hacking in October 1991 and at all 4 locations in November 1992. We acknowledge that any influences of thermoclines on vertical distributions of fish larvae and mesozooplankton may have occurred at finer depth scales than those examined here. For example, actual peaks in the concentrations of fish larvae and zooplankton may have been at depths between the 10 to 15 m strata sampled. Vertical distributions of plankton around thermoclines may be influenced on micro-scales (e.g. 1 to 2 m) (Owen 1989,

Tiselius et al. 1994). These scenarios could be tested with continuous sampling using a profiler (Kingsford & Murdoch 1998).

Taxon-specific vertical distributions of fish larvae and mesozooplankton were strong, indicating that they were responding to some biotic or abiotic component of their environment (e.g. water density, light intensity), other than thermal stratification. Larval diversity and abundance was generally greatest in the upper and mid-water column (5 to 30 m) and least near the bottom during daytime in stratified and unstratified waters. This daytime pattern, combined with the observations that fish larvae disperse throughout the entire water column at night, suggest that light intensity may be an important influence on their vertical distributions (see also Leis 1991b, Gray 1998). In contrast, this was not evident for zooplankton which displayed similar distributions day and night. It was not possible to determine what factors were most responsible for structuring the vertical distributions observed in this study. It is evident, however, that any modeling of interactions between fish larvae, zooplankton and thermoclines in these waters would be complex and would require fine-scale spatial and temporal resolution.

Trophic interactions

It has been argued that fish larvae may actively aggregate in thermoclines because their prey is often concentrated there (see Heath 1992, Röpke 1993), and this has lead to the belief that thermoclines are an important interface for trophic interactions and that the persistence and stability of these features can enhance larval survival (see Lasker 1975, Heath et al. 1988, Frank et al. 1989, Munk et al. 1989). We suggest that thermoclines may be of less importance to the trophic interactions and survival of fish larvae in waters where the physical stratification of the water column is highly variable from place-to-place and throughout short time intervals. Because of the instability and variable nature of thermoclines in coastal waters plankters may not respond to changes fast enough for this interface to be a critical feature. We found mesozooplankton to be most prevalent in the upper water column above thermoclines (when present) day and night, and therefore there may have been no need for fish larvae to aggregate in thermoclines in order to feed in these waters. We acknowledge that fish larvae may have been feeding on smaller zooplankton (e.g. copepod nauplii, Munk & Kiorboe 1985) that we did not consider. Nevertheless, fish larvae and zooplankton prey (*Penilia avirostris*) and predators (chaetognaths and copepods) were most concentrated in the upper strata, and

although their vertical distributions were not always concordant, they occurred in relatively high concentrations, and therefore fish larvae would encounter prey and predators at some time in this strata. Clearly, in the waters examined here the upper water column is the most important strata for trophic interactions, and future studies concerning trophic links in this environment need to be focused here. In particular, better resolution of small scale larval patchiness and links to food and predators is required, which will involve sampling smaller food items than done here.

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