

# Synchronicity between zooplankton biomass and larval fish concentrations along a highly flushed Tasmanian estuary: assessment using net and acoustic methods

ANA LARA-LOPEZ<sup>1,2\*</sup> AND FRANCISCO J. NEIRA<sup>1</sup>

<sup>1</sup>TASMANIAN AQUACULTURE AND FISHERIES INSTITUTE, UNIVERSITY OF TASMANIA, PO BOX 49, HOBART 7001, AUSTRALIA AND <sup>2</sup>AUSTRALIAN FISHERIES MANAGEMENT AUTHORITY, LEVEL 2 PEALS BUILDING, 38 VICTORIA PARADE, THURSDAY ISLAND, QLD 4875, AUSTRALIA

\*CORRESPONDING AUTHOR: analigia@yahoo.com

Received March 15, 2008; accepted in principle June 2, 2008; accepted for publication June 2, 2008; published online June 5, 2008

Corresponding editor: Roger Harris

*We examined the spatio-temporal synchronicity between zooplankton biomass and larval fish concentrations within a highly flushed system in northern Tasmania, Australia, combining the data from nets and acoustic methods obtained between October 2001 and November 2002. Zooplankton and larval fish data from nets were analysed in terms of water temperature, salinity and freshwater flow, while backscatter strength from an Acoustic Doppler Current Profiler (ADCP) was employed to complement zooplankton-net data and identify the likely areas of high secondary productivity. Zooplankton and fishes varied significantly across months, peaking simultaneously during late spring (November) at an average temperature of  $\sim 15^{\circ}\text{C}$ . Maximum zooplankton ( $20.5\text{ mgC}/\text{m}^3$ ) and fishes ( $874\text{ larvae}/100\text{ m}^3$ ) were recorded within mesohaline (5–17) and polyhaline (18–29) zones, respectively, also in spring. Peaks in zooplankton and larval fish occurred a month after peak freshwater flow, with temperature explaining variability better than did flow or salinity. The coupling of spring peaks in zooplankton biomass and larval fish implies that estuary-spawning fishes may have a fixed spawning period timed to increasing temperatures to ensure a match with abundant microplankton food supply. Backscatter strength complemented zooplankton biomass from nets, and could arguably be used as a proxy for zooplankton abundance even within “noisy” estuarine systems.*

## INTRODUCTION

Estuarine zooplankton play a significant role linking primary producers and higher trophic levels, as well as phytoplankton regulators and nutrient recyclers (Reeve, 1975; Day *et al.*, 1989; Capriulo *et al.*, 2002). For example, the spawning of estuarine fish species is often timed to coincide with peak zooplankton abundance to ensure abundant microplankton is available for the survival of their larval stages, and thus offset starvation-induced mortality (Harrison and Whitfield,

1990; Whitfield and Harrison, 1996). Moreover, the variability in zooplankton availability, mostly linked to environmental conditions, has been related to variability in larval fish mortality due to starvation (Hjort, 1926; Cushing, 1969, 1990; Fortier *et al.*, 1995; Brander *et al.*, 2001; Beaugrand *et al.*, 2003; Durant *et al.*, 2007). This has led to some fish species spreading their spawning effort over longer periods of time in areas where the availability of planktonic prey is highly variable in order to increase the chance of larval survival (Mertz and Myers, 1994; Durant *et al.*, 2007).

Research on zooplankton distribution and abundance patterns in marine ecosystems has advanced considerably since the first application of hydroacoustics (Flagg and Smith, 1989; Batchelder *et al.*, 1995; MacLennan and Holliday, 1996; Zimmerman and Biggs, 1999; Lavery *et al.*, 2002; Cabreira *et al.*, 2006). As a non-invasive technique, hydroacoustics provides real-time high-resolution, both quantitative and qualitative, data that cannot be obtained with traditional sampling methods. In addition, acoustics is also capable of revealing the complex dynamics of zooplankton, including responses to local oceanography both temporally and spatially (Weeks *et al.*, 1995; Lavery *et al.*, 2002). Unlike marine systems, however, hydroacoustics in estuaries and shallow marine areas has been employed mostly to study sediment dynamics, and relatively little attention has been given to biological processes (Thorne *et al.*, 1991; Hay and Sheng, 1992; Reichel and Nachtnebel, 1994; Roman *et al.*, 2001; Gartner, 2004).

This study was designed to assess the temporal and spatial synchronicity between zooplankton biomass and larval fish concentrations within the Tamar Estuary, a highly flushed estuary in northern Tasmania (Australia). We employed standard plankton nets to collect zooplankton and larval fish, as well as backscatter strength data from an Acoustic Doppler Current Profiler (ADCP) to complement zooplankton-net data and identify the likely areas of high zooplankton abundance. Zooplankton data were converted to biomass and, together with larval fish concentrations, analysed in terms of changes in temperature, salinity and freshwater flow. Finally, we briefly discuss whether acoustic backscatter strength can be used as a proxy of zooplankton biomass within highly flushed estuaries, noting that this is the first time that the ADCP technology has been applied in such variable systems.

## METHODS

### Study area

The study was conducted in the Tamar Estuary in northern Tasmania, one of the largest partially mixed, highly flushed systems in temperate Australia (Fig. 1). The estuary comprises one major winding course surrounded by sandbanks and rocky reefs in the lower reaches and fine sediment in the upper reaches, and three extensive shallow bays interconnected by channels as narrow as 300 m, e.g. Batman Bridge (Phillips, 1975; Bell, 1996). Two main tributaries, the North and South Esk rivers, discharge into the estuary draining a catchment area of ca. 11 600 km<sup>2</sup>, the largest in Tasmania

(Edgar *et al.*, 1999). The tidal regime is semidiurnal with a moderate diurnal inequality of an ~6-h flood and a 7-h ebb tide. Average tidal range is 3 m at Georgetown in the lower estuary and 3.5 m at Launceston in the upper estuary. The tidal force, coupled with the course's constrictions and directional changes, as well as uneven bathymetry, generate high flow velocities that can create strong upwelling, whirlpools, turbulence and hydraulic fronts (Phillips, 1975; Pringle, 1982; Bell, 1996).

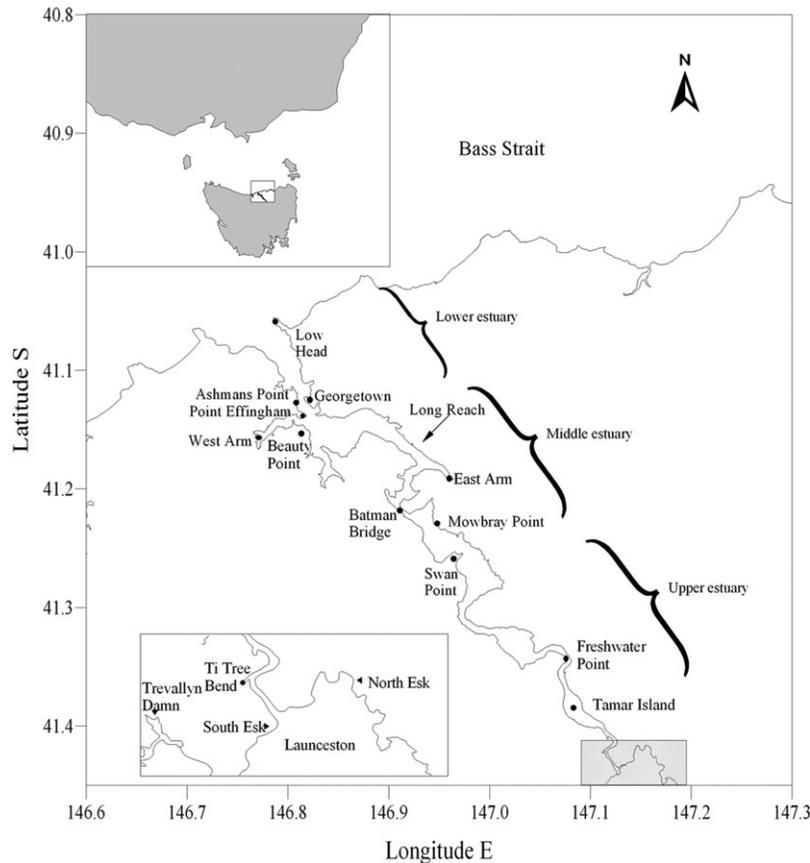
### Sampling regime and treatment of samples

A total of 186 plankton samples were obtained simultaneously with physical variables between October 2001 and November 2002 from randomly selected sites. Samples were collected monthly in the lower and middle estuary, and bi-monthly in the upper estuary (total = 14 surveys). Sampling in the lower estuary was omitted in November 2001, and in the December 2001–February 2002 period. Replicate samples were collected behind a 14-m steel hull prawn trawler using a bongo sampler consisting of 300 and 500 µm mesh plankton nets, each 0.6 m in diameter and 3 m in length. At each site, the sampler was deployed from the stern of the vessel and towed for 10 min at a depth of 5–10 m and speeds of 1.0–1.5 knots. Total water volume filtered during each tow (m<sup>3</sup>) was estimated using flowmeters (General Oceanics) attached inside the mouth of each net. All samples were fixed on board using 10% formalin–seawater and later preserved in 70% ethanol. Larval fish were removed from all samples and counted, and the total number added for the two nets and converted into concentrations, i.e. numbers per 100 m<sup>3</sup>. The entire non-fish zooplankton component collected in the 300 µm net was dried at 40°C for 48 h in a Contherm Series 5 oven, weighed in a Sartorius 1702MP8 electronic balance. The resultant dry weight (DW) was standardized to milligram per cubic metre and converted to biomass (mgC/m<sup>3</sup>) using the Wiebe equation (Wiebe, 1988):

$$\log(\text{DW}) = 0.499 + 0.991 \times \log(C) \quad (1)$$

where  $C$  is the biomass in mgC/m<sup>3</sup>.

Water column temperature (°C) and salinity by depth (m) were obtained with a Seabird Electronics SBE19 Conductivity–Temperature–Depth (CTD) profiler. Daily freshwater flow data from weather stations in the North Esk and South Esk rivers were obtained from the Australian Bureau of Meteorology and Hydro Tasmania, respectively, and averaged monthly for analyses.



**Fig. 1.** Geographical position of the Tamar Estuary in northern Tasmania, showing reference locations and the three main regions sampled during this study.

Acoustic backscatter strength ( $S_v$ ) was measured as a proxy of zooplankton biomass using a 600 kHz RDI Workhorse Rio Grande ADCP. The frequency of this ADCP emits a wavelength of  $\sim 2.5$  mm (if speed of sound = 1500 m/s). If acoustic waves are able to detect objects of one-quarter of their wavelength (Emery and Thomson, 1997; Sindlinger *et al.*, 2005), then the smallest size that the ADCP used in the study is able to detect is  $\sim 0.625$  mm, size which is within the range of abundant zooplankton such as copepods (Holliday and Pieper, 1980).

Acoustic data were obtained simultaneously with the plankton samples collected during October 2001–April 2002 and August–November 2002, using the ADCP attached below the vessel's water line. Acoustic data were unavailable for the period May–July 2002 due to unit malfunction. The ADCP, which records acoustic backscatter information approximately every second via the received signal strength indicator (RSSI) circuit, was left recording continuously during surveys. Data were averaged into 1-min intervals, with a vertical resolution of 100 bins, each 1 m deep, processed with

TRANSECT (RDI), and converted into backscatter strength ( $S_v$ , dB) using Deines's modified sonar equation (Deines, 1999):

$$S_v = C + 10 \log_{10} [(T_x + 273.16)R^2] - L_{\text{DBM}} - P_{\text{DBM}} + 2\alpha R + Kc(E - E_r) \quad (2)$$

where  $L_{\text{DBM}}$  refers to  $10 \log_{10}(\text{transmit pulse length})$  (m),  $P_{\text{DBM}}$   $10 \log_{10}(\text{transmit power})$  (W),  $T_x$  temperature of transducer ( $^{\circ}\text{C}$ ),  $R$  range along beam (slant range) to scatterers (m),  $\alpha$  sound absorption coefficient of water ( $\text{dB m}^{-1}$ ),  $E$  echo intensity derived from the RSSI (counts),  $E_r$  echo intensity reference level (counts).  $Kc$  conversion factor (dB), provided by the manufacturer RDI, and  $C$  is instrument constant, provided by the manufacturer RDI.

Sound absorption coefficient ( $\alpha$ ) was estimated using CTD data recorded at each site and following the equations of Francois and Garrison (Francois and Garrison, 1982a, b).

Values of Sv from the first two depth cells (1–2 m) was omitted due to noise created by the vessel's hull, whereas Sv from the subsequent 5 m was averaged for comparison with net-derived biomass. Spatio-temporal contour maps of mean Sv were created using SURFER<sup>®</sup> for the survey area to locate high Sv spots, and examined to ascertain whether they reflected regions of high zooplankton biomass identified from net collections.

### Data analyses

Replicate biomass samples (mgC/m<sup>3</sup>) and larval fish concentrations (larvae/100 m<sup>3</sup>) were averaged and log-transformed (ln) to account for heterogeneity of variance following Cochran's test. One-way ANOVA was performed to test for the temporal variation in zooplankton biomass only because parametric test assumptions to assess temporal variation in larval fish concentrations were not met. However, due to evident temporal variation in larval fish concentrations, this test was considered unnecessary. Spatial variation in zooplankton biomass and larval fish concentrations was examined only during high abundance periods, i.e. October–December 2001, and October and November 2002. All statistical analyses were performed using STATISTICA<sup>®</sup>.

Preliminary tests to analyse spatial variation revealed larger differences within sites (replicas) than among them, probably due to different factors such as the patchy distribution of zooplankton and net avoidance. Consequently, it was decided to compare mean zooplankton biomass and larval fish concentrations among estuary zones classified according to the Venice System of salinity: euhaline (30–36), polyhaline (18–29) and meso-oligohaline (0.5–17) (Anonymous, 1959; Bulger *et al.*, 1993). This classification system, based on salinity, is recommended for universal application and can be used to describe the distribution patterns of estuarine flora and fauna. Such classification has been widely used to describe distribution patterns of faunal assemblages as well as individual species within estuarine systems (Muylaert and Sabbe, 1999; Muylaert *et al.*, 2000; Mouny and Dauvin, 2002; Strydom *et al.*, 2003). Given the unbalanced data set derived from the different number of sites and zones sampled during the study (one to five sites per zone), one-way ANOVAs were utilized to examine the spatial variation of zooplankton biomass and larval fish concentrations among Venice zones for each month of the high abundance periods. Parametric test assumptions, i.e. normality and homogeneity of variance, were assessed using Cochran's test. Multiple stepwise regression analyses were performed to

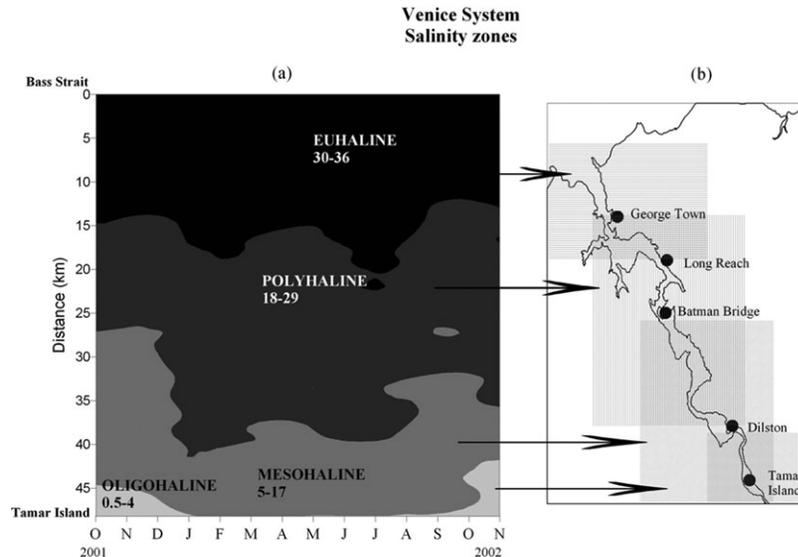
examine the association between physical variables, zooplankton biomass and larval fish distributions; data with a standard deviation of  $\pm 3$  from the mean were regarded as outliers and omitted from the analyses. All variables were log-transformed (ln) to account for heterogeneity in variance.

Predictive and functional (Fielding *et al.*, 2004) linear regressions were used to determine whether there was a significant relationship between zooplankton biomass and Sv. Predictive regressions minimize the sum of squares of the vertical or horizontal distances from the points to the regression line, whereas functional regressions measure the central trend of a distribution by minimizing the sum of products of the vertical and horizontal distance of each point from the line (Ricker, 1973).

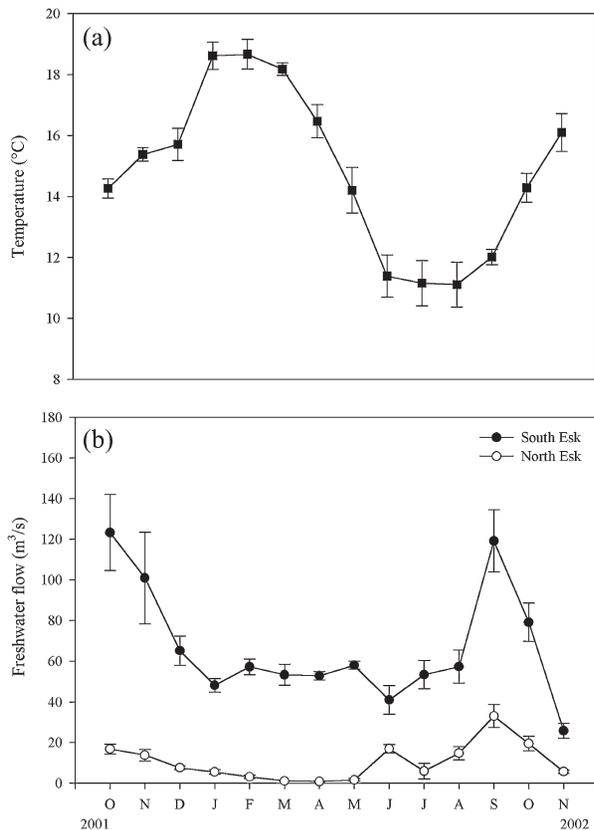
Zooplankton DW (mg/m<sup>3</sup>) was divided by  $4\pi$  to facilitate comparisons with other studies that have also employed ADCP backscatter strength. This standardization procedure follows the argument that target strength (=backscatter strength) can be expressed as  $Sv = \log_{10}(\sigma_s/4\pi)$ , where  $\sigma_s$  is the acoustical cross-sectional target area. Since biomass is approximately proportional to the target cross-sectional area, and hence to  $\sigma_s$ , the term  $\sigma_s$  can be substituted by biomass in DW thus becoming  $Sv = \log_{10}(DW/4\pi)$  (Flagg and Smith, 1989; Fielding *et al.*, 2004). Due to the high sound scattering of sediment and air bubbles (Stanton *et al.*, 1994; Coyle, 2000; Gartner, 2004), data that were considered to be affected by large sediment concentrations and/or air bubbles were excluded from the analyses.

## RESULTS

Mean salinity throughout the estuary ranged from 2.0 to 35.6, with the lowest salinities recorded in the upper reaches in November 2001 and October 2002. Temporal variation in salinity was evident in the boundary shifting of the Venice zones along the estuary, with the polyhaline (18–29) and mesohaline (5–17) zones experiencing most changes (Fig. 2a and b). Mean monthly temperatures increased from 14°C in October 2001 to 19°C in February 2002, before declining to a minimum of 11°C in August 2002 and later reaching 16°C in November 2002 (Fig. 3a). Highest and lowest mean freshwater flows (m<sup>3</sup>/s) in the South Esk occurred in October 2001 (123) and November 2002 (41), and were significantly greater than the highest (33, September 2002) and lowest (0.8, April 2002) flows recorded in the North Esk during the same period (Fig. 3b).



**Fig. 2.** (a) Temporal variation of the different Venice salinity zones along the Tamar Estuary between October 2001 and November 2002 and (b) geographical location of the Venice zones. Line patterns in (b) represent the area occupied by the salinity zones in the estuary during the sampling period.

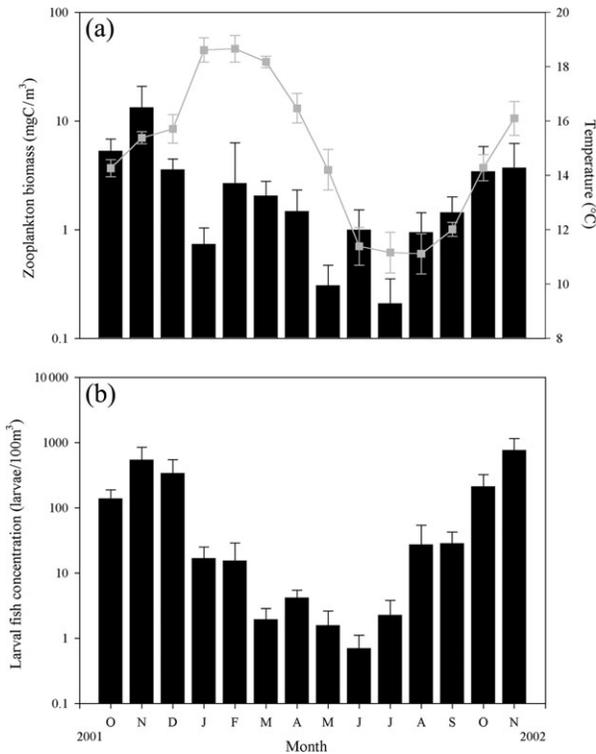


**Fig. 3.** Mean ( $\pm$  95% CI) monthly (a) temperature ( $^{\circ}$ C) along the Tamar Estuary and (b) freshwater flow ( $m^3/s$ ) from the North and South Esk rivers between October 2001 and November 2002.

Both zooplankton biomass and larval fish concentrations peaked in November 2001 ( $13.21 \text{ mgC}/m^3$ ;  $207 \text{ larvae}/100 \text{ m}^3$ ) and again in November 2002 ( $3.7 \text{ mgC}/m^3$ ;  $381 \text{ larvae}/100 \text{ m}^3$ ), when water temperatures were  $\sim 15^{\circ}\text{C}$ . Lowest mean monthly zooplankton biomass ( $0.20 \text{ mgC}/m^3$ ) and larval concentrations ( $0.7 \text{ larvae}/100 \text{ m}^3$ ) were recorded in July and June 2002, respectively (Fig. 4a and b).

Mean zooplankton biomass varied significantly across seasons ( $P < 0.001$ ), while spatial variation among the three main Venice salinity zones was significant only in October 2002 (Table I). Likewise, the mean larval fish concentrations did not vary significantly among Venice zones during the high abundance periods except in October 2002 (Table II). The lack of spatial variation in zooplankton biomass and larval fish concentrations was also evident during the other months, when differences between salinity zones were not significant.

Highest and lowest overall mean zooplankton biomasses were recorded within the mesohaline zone in November 2001 ( $20.5 \text{ mgC}/m^3$ ) and August 2002 ( $0.05 \text{ mgC}/m^3$ ). Peaks in zooplankton biomass in the euhaline zone occurred in October 2001 ( $5.6 \text{ mgC}/m^3$ ) and 2002 ( $7.11 \text{ mgC}/m^3$ ), whereas peaks in the polyhaline zone occurred in November 2001 ( $6.7 \text{ mgC}/m^3$ ) and 2002 ( $5.6 \text{ mgC}/m^3$ ) (Fig. 5a–c). Highest and lowest larval fish concentrations were recorded in the polyhaline zone in November 2002 ( $874 \text{ larvae}/100 \text{ m}^3$ ) and June 2001 ( $0.4 \text{ larvae}/100 \text{ m}^3$ ), whereas peak larval



**Fig. 4.** Mean (+95% CI) monthly (a) zooplankton biomass (mgC/m<sup>3</sup>; log-scale) and temperature (°C) and (b) larval fish concentrations (larvae/100 m<sup>3</sup>; log-scale) in the Tamar Estuary between October 2001 and November 2002.

*Table I: Results from one-way ANOVAs (ln-transformed data) for temporal variation of biomass (mgC/m<sup>3</sup>), and for spatial variation during peak biomass season*

	SS	df	MS	F	P	Tukey test
Temporal	136.35	3	45.45	21.94	***	S U A W
Spatial	SS	df	MS	F	P	
Oct 2001	0.02	2	0.01	0.05	NS	
Nov 2001	5.09	2	2.54	2.53	NS	
Dec 2001	0.06	1	0.06	2.41	NS	
Oct 2002	4.37	2	2.19	6.43	**	E P M
Nov 2002	2.21	1	2.21	4.66	NS	

NS, not significant. Tukey test abbreviations: S, spring; U, summer; A, autumn; W, winter; E, euhaline; P, polyhaline; M, meso-oligohaline. \*\**P* < 0.01; \*\*\**P* < 0.001.

concentrations in the euhaline and meso-oligohaline zones occurred in November 2002 (651 larvae/100 m<sup>3</sup>) and November 2001 (553 larvae/100 m<sup>3</sup>) (Fig. 6a-c).

*Table II: Results from one-way ANOVA (ln-transformed data) for spatial variation of larval fish concentrations (larvae/100 m<sup>3</sup>) during peak biomass season*

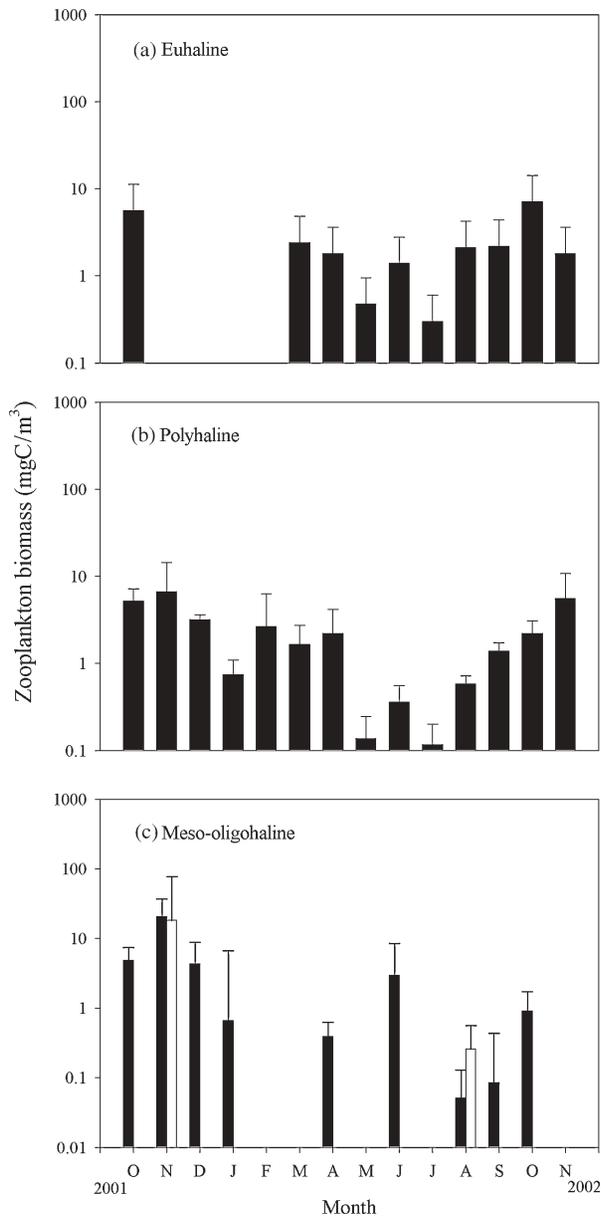
	SS	df	MS	F	P	Tukey test
Oct 2001	5.06	2.00	2.53	3.27	NS	
Nov 2001	4.81	2.00	2.40	3.61	NS	
Dec 2001	2.73	2.00	1.36	2.98	NS	
Oct 2002	23.50	2.00	11.75	9.84	**	E P M
Nov 2002	0.90	1.00	0.90	0.99	NS	

NS, not significant. Tukey test abbreviations: E, euhaline; P, polyhaline; M, meso-oligohaline. \*\**P* < 0.01.

Multiple linear regressions showed that 46% of the zooplankton biomass variability was explained by physical variables, with water temperature being the most significant (*P* < 0.001) followed by freshwater flow (Table III). Moreover, zooplankton biomass, temperature and freshwater flow explained 70% of the variability in larval fish concentrations (*P* < 0.001), with water temperature and zooplankton biomass being the most significant factors. Salinity, in contrast, was not significant (Table IV).

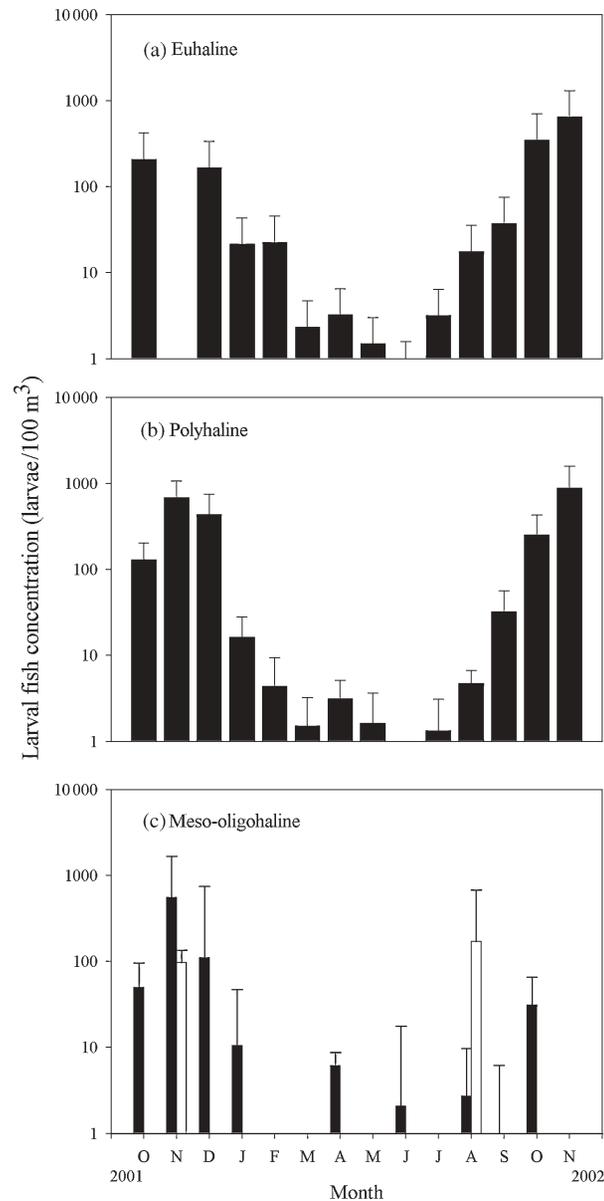
The Sv value showed a significant, positive linear relationship with zooplankton biomass (*R* = 0.66; *r*<sup>2</sup> = 0.43; *P* < 0.001; *n* = 71). Resulting equations for the predictive (P) and functional (F) regressions were: ZB(P) = 0.038(Sv) + 0.303 and ZB(F) = 0.057(Sv) + 1.55, respectively (Fig. 7). In general, higher Sv was recorded during October, November, December 2001 and September 2002. The mean Sv increased with distance from estuary mouth and exhibited a difference of ~10 dB between Venice zones, i.e. -80, -70 and -60 dB in the euhaline, polyhaline and meso-oligohaline zones, respectively. Changes in mean Sv within the euhaline (-80 to -70 dB) and meso-oligohaline (-60 to -40 dB) zones were larger than those recorded within the polyhaline zone, where no increment in Sv with distance was evident except for patches of different magnitude unevenly distributed along the zone (Fig. 8).

Overall, most of the areas where high zooplankton biomass was sampled coincided with areas of high Sv (Fig. 8). For example, high Sv values (-40 dB) matched highest biomass obtained in the upper estuary in November 2001 (27.7 mgC/m<sup>3</sup>), whereas low Sv values (-80 to -75 dB) match low biomass (0.3-0.5 mgC/m<sup>3</sup>) obtained in the polyhaline zone in January and August 2002. However, relatively high Sv values (-65 to -60 dB) were also recorded for low biomass, such as that obtained along the polyhaline zone in March 2002 (0.4 mgC/m<sup>3</sup>) and April 2002 (0.7 mgC/m<sup>3</sup>), whereas



**Fig. 5.** Mean (+95% CI) monthly zooplankton biomass (mgC/m<sup>3</sup>, log-scale) in the Tamar Estuary at the different Venice salinity zones. (c) Mesohaline (black bars) and oligohaline (white bars).

Sv values did not reflect low biomass observed throughout the estuary in September 2002. In general, larval fish concentrations followed a similar spatio-temporal pattern to that of zooplankton biomass with high larval concentrations mostly coinciding with high biomass (Fig. 8). However, during the peak season, high larval concentrations did not always followed the same spatial distribution with the highest concentration recorded in the polyhaline zone during November 2002 (833 larvae/100 m<sup>3</sup>) when biomass was only 11 mgC/m<sup>3</sup> (Fig. 8b).



**Fig. 6.** Mean (+95% CI) monthly larval fish concentrations (larvae/100 m<sup>3</sup>, log-scale) in the Tamar Estuary at the different Venice salinity zones. (c) Mesohaline (black bars) and oligohaline (white bars).

## DISCUSSION

### Synchronicity and links with environmental variables

Our study showed a close correspondence between peaks in zooplankton biomass and larval fish concentrations in the Tamar Estuary, with zooplankton contributing significantly to the variability in larval concentrations. This finding suggests that the timing in the

*Table III: Stepwise multiple linear regression analysis of biomass variability and environmental factors*

$R = 0.70$	adj $R^2 = 0.46$ Beta	$F = 20.4$ B	*** $P$
Temperature	0.50	0.13	***
Freshwater flow	0.25	0.01	**
Salinity	0.14	0.01	NS

adj $R^2$ , adjusted correlation coefficient;  $F$ ,  $F$ -statistics, Beta, individual standardized regression coefficient; B, raw relation coefficients; NS, not significant.

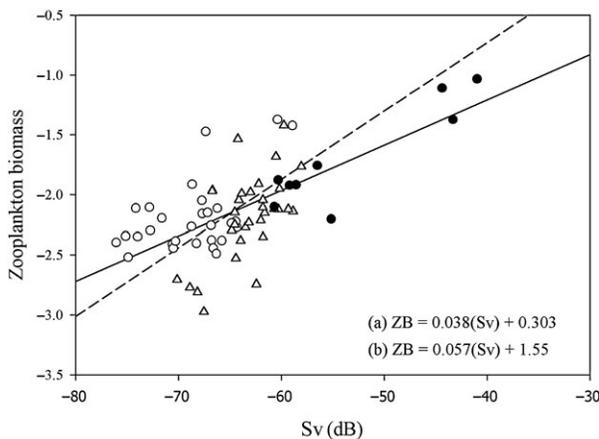
\*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

*Table IV: Stepwise multiple linear regression analysis of larval fish concentrations versus biomass and environmental factors*

$R = 0.85$	adj $R^2 = 0.70$ Beta	$F = 36.8$ B	*** $P$
Temperature	0.37	3.75	***
Zooplankton biomass	0.26	0.71	**
Freshwater flow	-0.16	-0.72	*
Salinity	-0.07	-0.26	NS

adj $R^2$ , adjusted correlation coefficient;  $F$ ,  $F$ -statistics; Beta, individual standardized regression coefficient; B, raw relation coefficients; NS, not significant.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



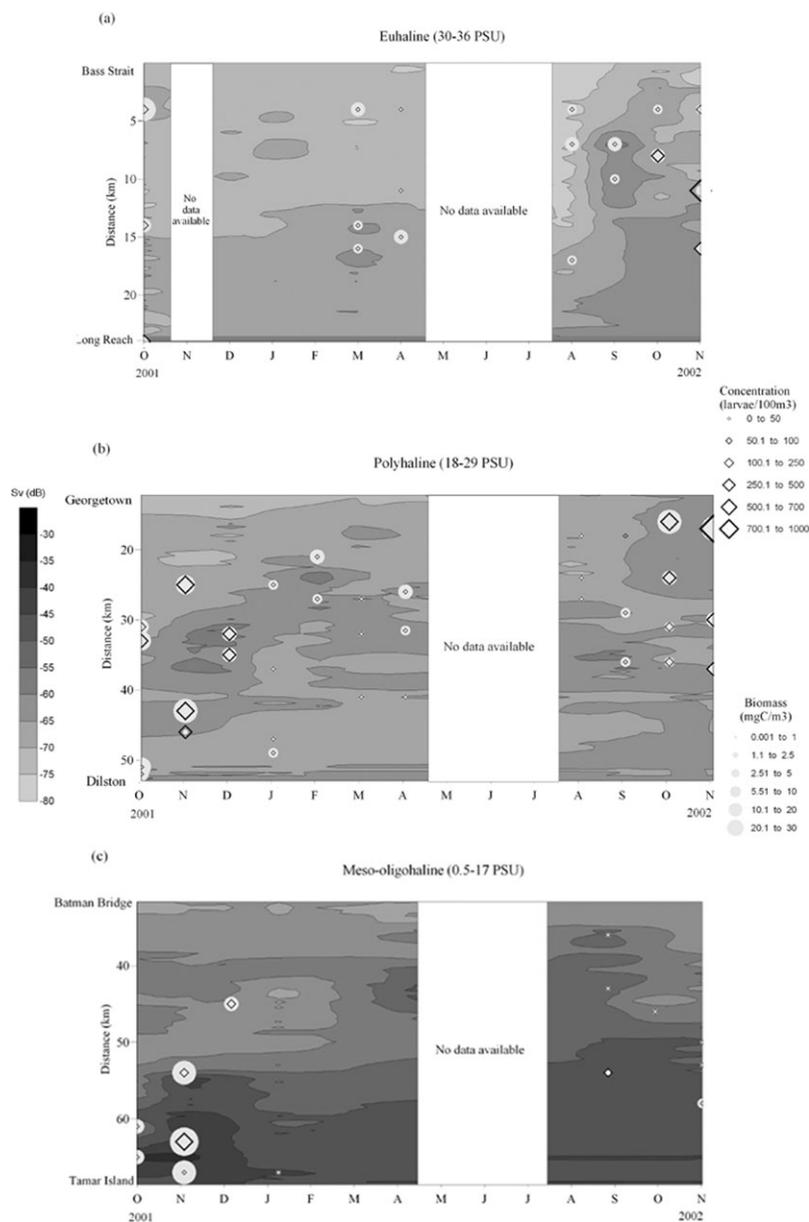
**Fig. 7.** Predictive (a, continuous line) and functional (b, dashed line) linear regressions fitted to the relationship between Sv and zooplankton biomass ( $ZB = \log[DW/4\pi]$ ).  $R = 0.66$ ;  $r^2 = 0.43$ . Symbols indicate Venice zone: open circle, euhaline; open triangle, polyhaline; filled circle, meso-oligohaline.

occurrence of larval fish within this highly flushed system is closely linked to zooplankton peak abundance. Moreover, the consistency of the November peaks in larval concentrations during this and other similar studies within this estuary (Raudzens, 2007) implies that a number of estuarine fish species may have fixed spawning periods to ensure a match between larvae and

microplankton food supply as in other estuaries (Cushing, 1969, 1975, 1990; Bye, 1984; Fortier *et al.*, 1995; Brander *et al.*, 2001; Beaugrand *et al.*, 2003). These include common estuarine-spawning species such as *Engraulis australis* and *Parablennius tasmanianus*, and also some gobiids (Neira *et al.*, 1992; Lara Lopez and Neira, in preparation). While spawning synchronicity following an increase in temperature and associated zooplankton abundance has also been reported for estuarine fishes in other temperate estuaries (e.g. Bye, 1984; de Lafontaine *et al.*, 1984; Drake and Arias, 1991; Witting *et al.*, 1999), the zooplankton-larval fish match described for the Tamar Estuary contrasts with the mismatch described for estuaries such as the Newport River in eastern USA (Thayer *et al.*, 1974) and Hopkins River in south-eastern Australia (Newton, 1996), where zooplankton peaked 1–2 months before larval fish.

The spatial distribution of zooplankton biomass and larval concentrations did not differ markedly between Venice zones identified along the Tamar Estuary during the high abundance seasons (October–December 2001 and October–November 2002). This lack of spatial variability contrasts with the situation reported for temperate estuaries in Europe and South Africa, where significant differences in zooplankton biomass and/or larval fish distributions have been recorded either in mesohaline or in oligohaline zones (Sautour and Castel, 1995; Mouny and Dauvin, 2002; Strydom *et al.*, 2003). Several factors could explain the low spatial variability, including strong tidal currents redistributing plankton more uniformly along the estuary and the shifting of zone boundaries. The latter appears to be an important factor, given that the polyhaline zone was the only zone that was sampled during all months and extended through much of the estuary. In contrast, the euhaline zone was not sampled during summer, and the mesohaline and oligohaline zones fell outside the sampling area during the dry season, i.e. February to July 2002. In any case, a spatial match between biomass (food source) and larval fish concentrations in the Tamar is likely to increase the survival of larval fishes (Napp *et al.*, 1996; Chick and Van den Avyle, 1999; Durant *et al.*, 2007), particularly when strong tidal currents redistribute prey items uniformly, thereby increasing the chances of larvae finding food.

The marked seasonal changes in zooplankton biomass and larval fish concentrations observed throughout the Tamar Estuary were largely explained by changes in water temperature. The timing of zooplankton and larval concentration peaks (November 2001 and 2002), when water temperatures were  $\sim 15^\circ\text{C}$ , match those recorded for zooplankton and larval fishes in late spring in various temperate bays and



**Fig. 8.** Horizontal contours of mean Sv (dB) along the (a) euhaline, (b) polyhaline and (c) meso-oligohaline zones in the Tamar Estuary between October 2001 and November 2002. Mean zooplankton biomass ( $\text{mgC}/\text{m}^3$ , grey circles) and larval fish concentrations ( $\text{larvae}/100\text{m}^3$ , diamonds) have been superimposed at each sampling site. Sv data were not available for the period of May–July 2002 due to instrument malfunction.

estuaries of mainland Australia (Steffe and Pease, 1988; Neira *et al.*, 1992; Newton, 1996) and elsewhere in the world (Sautour and Castel, 1995; Wooldridge, 1999; Froneman, 2001, 2004; Capriulo *et al.*, 2002; Mouny and Dauvin, 2002; Roman *et al.*, 2005). The close relationship between zooplankton and larval concentrations with temperature may reflect the influence of temperature on larval recruitment and seasonal

fluctuations of zooplankton populations (Day *et al.*, 1989; Mouny and Dauvin, 2002).

Peaks in zooplankton biomass and larval fish during this study occurred 1 month after peak freshwater flows, and are thus likely to be associated with an increase in nutrients and phytoplankton productivity following freshwater input (Wooldridge, 1999; Froneman, 2004). However, the association between zooplankton biomass

and larval concentration with freshwater flow was not as significant as with water temperature. The latter finding could well be due to freshwater flow influencing a number of other environmental variables (covariates), such as nutrient and sediment concentrations, displacement of salinity fields, residence time and other hydrodynamic factors that may directly affect the distribution of planktonic organisms (Allanson and Read, 1995; Adams *et al.*, 1999; Wooldridge, 1999; Froneman, 2001, 2004; Kimmerer, 2002). It is thus possible that freshwater flow may only indirectly influence the changes in zooplankton biomass and larval concentrations, making it difficult to statistically distinguish any direct relationship with freshwater flow (Kimmerer, 2002). However, the lag between peaks in freshwater flow and those in zooplankton and larval fish may have also affected the outcome of the statistical analyses yielding a less significant result.

Unlike the close association with temperature, our results showed that zooplankton biomass and larval concentrations were not associated with salinity either spatially or temporarily. These findings are not surprising since they reflect the fact that salinity mainly influences plankton distribution at the species rather than community level, which is in turn attributed to species-specific behaviour and tolerance to stress from salinity changes (Day *et al.*, 1989; Muylaert *et al.*, 2000; Louge *et al.*, 2002; Mouny and Dauvin, 2002; Seuront, 2006).

Almost 54% of the temporal variability in zooplankton biomass in the Tamar Estuary could not be explained by temperature, salinity and freshwater flow combined. However, it is likely that factors not considered during this study, such as chlorophyll *a*, turbidity, physical instabilities and/or predation rates, could have contributed to this unexplained variability (Froneman, 2001, 2004; North and Houde, 2001; Roman *et al.*, 2001; Capriulo *et al.*, 2002; Valle-Levinson *et al.*, 2003; Kimmel and Roman, 2004; Roman *et al.*, 2005). For example, our peaks in zooplankton biomass in November may be timed to coincide with peaks in chlorophyll *a*, which in the Tamar have also been observed around that time (Greg Dowson, DPIW, personal communication), thereby matching simultaneous zooplankton and chlorophyll *a* peaks reported for other estuaries (Ketchum, 1983; Froneman, 2001). In contrast to zooplankton biomass, 70% of the variability in larval fish concentrations could be explained by a combination of temperature, freshwater flow and zooplankton biomass, with factors such as predation, turbidity and physical instabilities likely to contribute to some of the unexplained variability (Frank and Leggett, 1982; Roper, 1986; Fancett and Jenkins, 1988; Bailey and Houde, 1989; Newton, 1996; Houde, 1997; Esteves

*et al.*, 2000; Capriulo *et al.*, 2002; Strydom *et al.*, 2003; Roman *et al.*, 2005).

### Backscatter strength as a proxy of zooplankton biomass

This constitutes possibly the first study to employ ADCP-derived backscatter intensity to examine zooplankton dynamics within a highly flushed estuarine system. The close relationship between log-transformed zooplankton DW and observed backscatter strength (Sv) parallels that reported in several sea-based studies, despite the difference in acoustic frequency and sampling techniques (Batchelder *et al.*, 1995; Zimmerman and Biggs, 1999; Wade and Heywood, 2001; Fielding *et al.*, 2004). Although calibration between nets and ADCP produces data of no better quality than nets due to inherent errors in sampling techniques (e.g. net avoidance, differences in volume sampled from nets and acoustics, background noise, uncertainty in towing depths, etc), the large increase in spatial and temporal resolution, as well as relative cost and speed of an acoustic approach, outweighs the problems of calibration between nets and ADCP (Holliday and Pieper, 1980, 1995; Holliday *et al.*, 1989).

In general, we found that high Sv areas matched areas of high zooplankton biomass derived from nets except in the euhaline zone in September 2002, and the polyhaline zone in March, April and September 2002. This lack of correspondence was also reflected in the variance observed in the linear relationship between Sv and zooplankton biomass. Several factors may have contributed to this variance, namely (i) intense rainfall and strong winds (>39 knots) generating air bubbles during September 2002, as well as presence of dense swarms of large jellyfishes clogging plankton nets during March–April 2002; (ii) difference in volume sampled and sample type (continuous versus discrete sampling) and (iii) patchy distribution of zooplankton (Costello *et al.*, 1989).

Unlike zooplankton biomass, Sv increased steadily with distance from estuary mouth, with the euhaline, polyhaline and meso-ohalohaline zones differing by ~10 dB. This increment in Sv could be mainly due to an increase in the amount of sediments upstream, which may have also led to the spread of the data in the regressions. Since sediments in the Tamar Estuary range from coarse marine sand in the lower-middle sections (to ~30 km upstream) to small mud particles <0.05 mm in the middle-upper sections (to ~65 km upstream), an increase in suspended sediments due to their low settling velocity (Foster *et al.*, 1986) upstream could likely cause the Sv increase. Furthermore, while

the size of sediment particles in the upper reaches is smaller than that detectable with a 600 kHz ADCP, it is highly likely that the large amounts of suspended sediment in the Tamar Estuary allowed the ADCP to detect them (Sindlinger *et al.*, 2005).

Despite Sv being affected by other factors, such as high upstream sediment concentrations, air bubbles and turbulent currents, our ADCP-measured Sv complemented zooplankton biomass from nets, particularly during the high zooplankton biomass period. While it is not possible to distinguish a change in particle size from a change in abundance with single frequency instruments (Holliday, 1992), the instrument was able to detect larger zooplankters (mostly copepods) as opposed to small particle sediments during the high biomass season in the upper estuary. Moreover, the net-ADCP combination allowed a better indication of the zooplankton distribution than that provided individually by either nets or ADCP. Despite these encouraging results, caution is still needed when interpreting Sv from a single frequency instrument such as the ADCP (MacLennan and Holliday, 1996; Fielding *et al.*, 2004), especially in estuaries like the Tamar where several noise sources may affect backscatter strength. In addition, while backscatter strength could potentially be used as a proxy of zooplankton abundance, there are important limitations in the use of single-frequency acoustic systems (Holliday, 1992). Such limitations could be overcome by using multi-frequency instruments, which have the advantage of detecting both changes in size and abundance (Holliday, 1992). In any case, direct sampling techniques should still be employed in combination with acoustic methods to allow a better interpretation of plankton dynamic processes (Costello *et al.*, 1989; Sutor *et al.*, 2005).

## ACKNOWLEDGEMENTS

Many thanks to all staff and volunteers from the AMC and the University of Tasmania (UTas) who helped during the project. Greg Dowson from the Tasmanian Department of Primary Industry and Water (DPIW) kindly provided chlorophyll *a* data. Hydro Tasmania allowed us to use the ADCP unit and, with the Australian Bureau of Meteorology, provided the freshwater flow data. This research formed part of the PhD dissertation of the senior author (A.L.L.) at UTas.

## FUNDING

This research was funded by the Natural Heritage Trust (NHT), the Australian Maritime College (AMC) and

the Upper Tamar River Improvement Authority. Many thanks to the Tamar Region Natural Resources Management Strategy (NRMS—Tasmania) for facilitating the way to obtain NHT funding.

## REFERENCES

- Adams, J., Bate, G. and O'Callagan, M. (1999) Estuarine microalgae. In Allanson, B. R. and Baird, D. (eds), *Estuaries of South Africa*. Cambridge University Press, Cambridge, UK, pp. 100–118.
- Allanson, B. R. and Read, G. H. L. (1995) Further comment on the response of eastern Cape province estuaries to variable freshwater inflows. *South Afr. J. Aquat. Sci.*, **21**, 56–70.
- Anonymous (1959) Symposium on the classification of brackish waters. *Arch. Oceanogr. Limnol.*, **11**, 243–248.
- Bailey, K. M. and Houde, E. D. (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.*, **25**, 1–83.
- Batchelder, H. P., Vankeuren, J. R., Vaillancourt, R. *et al.* (1995) Spatial and temporal distributions of acoustically estimated zooplankton biomass near the marine light-mixed layers station (59°30'N, 21°00'W) in the north Atlantic in May 1991. *J. Geophys. Res. Oceans*, **100**, 6549–6563.
- Baugrand, G., Brander, K. M., Lindley, J. A. *et al.* (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.
- Bell, K. N. (1996) Foraminiferan faunas of the River Tamar and Port Dalrymple, Tasmania: a preliminary survey. *Rec. Queen Vic. Mus.*, **102**, 1–25.
- Brander, K. M., Dickson, R. R. and Shepherd, J. G. (2001) Modelling the timing of plankton production and its effect on recruitment of cod (*Gadus morhua*). *ICES J. Mar. Sci.*, **58**, 962–966.
- Bulger, A. J., Hayden, B. P., Monaco, M. E. *et al.* (1993) Biologically-based estuarine salinity zones derived from a multivariate-analysis. *Estuaries*, **16**, 311–322.
- Bye, V. J. (1984) The role of environmental factors in the timing of reproductive cycles. In Potts, G. W. and Wootton, R. J. (eds), *Fish Reproduction: Strategies and Tactics*. Academic Press, London, pp. 187–205.
- Cabreira, A. G., Madirolas, A., Colombo, G. A. *et al.* (2006) Acoustic study of the Rio de la Plata estuarine front. *ICES J. Mar. Sci.*, **63**, 1718–1725.
- Capriulo, G. M., Smith, G., Troy, R. *et al.* (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. *Hydrobiologia*, **475**, 263–333.
- Chick, J. H. and Van den Avyle, M. J. (1999) Zooplankton variability and larval striped bass foraging: Evaluating potential match/mismatch regulation. *Ecol. Appl.*, **9**, 320–334.
- Costello, J. H., Pieper, R. E. and Holliday, D. V. (1989) Comparison of acoustic and pump sampling techniques for the analysis of zooplankton distributions. *J. Plankton Res.*, **11**, 703–709.
- Coyle, K. O. (2000) Acoustic estimates of zooplankton biomass and distribution: application of canonical correlation to scaling of multi-frequency acoustic data. *Can. J. Fish. Aquat. Sci.*, **57**, 2306–2318.
- Cushing, D. H. (1969) Regularity of spawning season of some fishes. *J. Conseil*, **33**, 81.
- Cushing, D. H. (ed.) (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge, pp. 278.
- Cushing, D. H. (1990) Plankton production and year-class strength in fish populations—an update of the match mismatch hypothesis. *Adv. Mar. Biol.*, **26**, 249–293.

- Day, J. W., Hall, C. A. S., Kemp, W. M. *et al.* (eds) (1989) *Estuarine Ecology*. Wiley, New York, pp. 558.
- de Lafontaine, Y., Sinclair, M., El-Sabh, M. I. *et al.* (1984) Temporal occurrence of ichthyoplankton in relation to hydrographic and biological variables at a fixed station in the St Lawrence Estuary. *Estuarine Coastal Mar. Sci.*, **18**, 177–190.
- Deines, K. L. (1999) *Backscatter Estimation Using Broadband Acoustic Doppler Current Profilers*. RD Instruments, San Diego, CA.
- Drake, P. and Arias, A. M. (1991) Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S.W. Spain). *J. Fish Biol.*, **39**, 245–263.
- Durant, J. M., Hjermann, D. O., Ottersen, G. *et al.* (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.*, **33**, 271–283.
- Edgar, G. J., Barrett, N. and Graddon, D. J. (1999) A classification of Tasmanian estuaries and assessment of their conservation significance using ecological and physical attributes, population and land use. *Report No. 0724647546*. Tasmanian Aquaculture and Fisheries Institute, Taroona, Tasmania.
- Emery, W. J. and Thomson, R. E. (eds) (1997) *Data Analysis Methods in Physical Oceanography*. Kidlington, New York, pp. 634.
- Esteves, E., Pina, T., Chicharo, M. A. *et al.* (2000) The distribution of estuarine fish larvae: nutritional condition and co-occurrence with predators and prey. *Acta Oecol. Int. J. Ecol.*, **21**, 161–173.
- Fancett, M. S. and Jenkins, G. P. (1988) Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. *J. Exp. Mar. Biol. Ecol.*, **116**, 63–77.
- Fielding, S., Griffiths, G. and Roe, H. S. J. (2004) The biological validation of ADCP acoustic backscatter through direct comparison with net samples and model predictions based on acoustic-scattering models. *ICES J. Mar. Sci.*, **61**, 184–200.
- Flagg, C. N. and Smith, S. L. (1989) On the use of the Acoustic Doppler Current Profiler to measure zooplankton abundance. *Deep-Sea Res. Part I Oceanogr.*, **36**, 455–474.
- Fortier, L., Ponton, D. and Gilbert, M. (1995) The match mismatch hypothesis and the feeding success of fish larvae in ice-covered Southeastern Hudson-Bay. *Mar. Ecol. Prog. Ser.*, **120**, 11–27.
- Foster, D. N., Nittim, R. and Walker, J. (1986) Tamar River Siltation Study. *Report No. 85/07*. The University of New South Wales, Water Research Laboratory, Manly Vale, NSW.
- Francois, R. E. and Garrison, G. R. (1982a) Sound absorption based on ocean measurements. Part I: pure water and magnesium sulphate contributions. *J. Acoust. Soc. Am.*, **72**, 896–907.
- Francois, R. E. and Garrison, G. R. (1982b) Sound absorption based on ocean measurements. Part II: boric acid contribution and equation for total absorption. *J. Acoust. Soc. Am.*, **72**, 1879–1890.
- Frank, K. T. and Leggett, W. C. (1982) Reciprocal oscillations in densities of larval fish and potential predators: a reflection of present or past predation. *Can. J. Fish. Aquat. Sci.*, **42**, 1841–1849.
- Froneman, P. W. (2001) Seasonal changes in zooplankton biomass and grazing in a temperate estuary, South Africa. *Estuarine Coastal Mar. Sci.*, **52**, 543–553.
- Froneman, P. W. (2004) Zooplankton community structure and biomass in a southern African temporarily open/closed estuary. *Estuarine Coastal Mar. Sci.*, **60**, 125–132.
- Gartner, J. W. (2004) Estimating suspended solids concentrations from backscatter intensity measured by Acoustic Doppler Current Profiler in San Francisco Bay, California. *Mar. Geol.*, **211**, 169–187.
- Harrison, T. D. and Whitfield, A. K. (1990) Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *South Afr. J. Zool.*, **25**, 161–168.
- Hay, A. E. and Sheng, J. Y. (1992) Vertical profiles of suspended sand concentration and size from multifrequency acoustic backscatter. *J. Geophys. Res. Oceans*, **97**, 15661–15677.
- Hjort, J. (1926) Fluctuations in the year classes of important food fishes. *J. Conseil Int. Explor. Mer*, **1**, 5–38.
- Holliday, D. V. (1992) Zooplankton acoustics. In Desai, B. N. (ed.), *Oceanography of the Indian Ocean*. Oxford & IBH Publishing Co. Pvt, Ltd, New Delhi, pp. 733–740.
- Holliday, D. V. and Pieper, R. E. (1980) Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. *J. Acoust. Soc. Am.*, **61**, 135–146.
- Holliday, D. V. and Pieper, R. E. (1995) Bioacoustical oceanography at high-frequencies. *ICES J. Mar. Sci.*, **52**, 279–296.
- Holliday, D. V., Pieper, R. E. and Kleppel, G. S. (1989) Determination of zooplankton size and distribution with multifrequency acoustic technology. *J. Conseil Int. Explor. Mer*, **46**, 52–61.
- Houde, E. D. (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. *J. Fish Biol.*, **51**, 52–83.
- Ketchum, B. H. (ed.) (1983) *Estuaries and Enclosed Seas*. Elsevier Scientific Pub. Co., Amsterdam, pp. 500.
- Kimmel, D. G. and Roman, M. R. (2004) Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. *Mar. Ecol. Prog. Ser.*, **267**, 71–83.
- Kimmerer, W. J. (2002) Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Mar. Ecol. Prog. Ser.*, **243**, 39–55.
- Lavery, A. C., Stanton, T. K., McGehee, D. E. *et al.* (2002) Three-dimensional modelling of acoustic backscattering from fluid-like zooplankton. *J. Acoust. Soc. Am.*, **111**, 1197–1210.
- Lougee, L. A., Bollens, S. M. and Avent, S. R. (2002) The effects of haloclines on the vertical distribution and migration of zooplankton. *J. Exp. Mar. Biol. Ecol.*, **278**, 111–134.
- MacLennan, D. N. and Holliday, D. V. (1996) Fisheries and plankton acoustics: past, present and future. In Simmonds, E. J. and MacLennan, D. N. (eds), *ICES International Symposium: Fisheries and Plankton Acoustics*. Academic Press, Aberdeen, Scotland, pp. 513–516.
- Mertz, G. and Myers, R. (1994) Match/mismatch predictions of spawning duration versus recruitment variability. *Fish. Oceanogr.*, **3**, 236–245.
- Mouny, P. and Dauvin, J. C. (2002) Environmental control of mesozooplankton community structure in the Seine estuary (English Channel). *Oceanol. Acta*, **25**, 13–22.
- Muylaert, K. and Sabbe, K. (1999) Spring phytoplankton assemblages in and around the maximum turbidity zone of the estuaries of the Elbe (Germany), the Schelde (Belgium/The Netherlands) and the Gironde (France). *J. Mar. Syst.*, **22**, 133–149.
- Muylaert, K., Sabbe, K. and Vyverman, W. (2000) Spatial and temporal dynamics of phytoplankton communities in a freshwater tidal estuary (Schelde, Belgium). *Estuarine Coastal Mar. Sci.*, **50**, 673–687.
- Napp, J. M., Incze, L. S., Ortner, P. B. *et al.* (1996) The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fish. Oceanogr.*, **5**, 19–38.
- Neira, F. J., Potter, I. C. and Bradley, J. S. (1992) Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. *Mar. Biol.*, **112**, 1–16.

- Newton, G. M. (1996) Estuarine ichthyoplankton ecology in relation to hydrology and zooplankton dynamics in a salt-wedge estuary. *Mar. Freshw. Res.*, **47**, 99–111.
- North, E. W. and Houde, E. D. (2001) Retention of white perch and striped bass larvae: biological–physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries*, **24**, 756–769.
- Phillips, A. W. (1975) The establishment of *Spartina* in the Tamar Estuary, Tasmania. *Papers Proc. R. Soc. Tasm.*, **109**, 65–75.
- Pringle, A. W. (1982) Tidal immersion of the Tamar Estuary *Spartina* Marsh, Tasmania Australia. *Papers Proc. R. Soc. Tasm.*, **116**, 143–152.
- Raudzens, E. (2007) Spring-summer larval fish assemblage in waters outside the Tamar Estuary in northern Tasmania. Master in Science, Australian Maritime College.
- Reeve, M. R. (1975) The ecological significance of the zooplankton in the shallow subtropical waters of South Florida. In Cronin, E. (ed.), *Estuarine Research: Chemistry, Biology and the Estuarine System*. Academic, New York, pp. 352–371.
- Reichel, G. and Nachtnebel, H. P. (1994) Suspended sediment monitoring in a fluvial environment: advantages and limitations applying an Acoustic Doppler Current Profiler. *Water Res.*, **28**, 751–761.
- Ricker, W. E. (1973) Linear regressions in fishery research. *J. Fish. Res. Board Can.*, **30**, 409–434.
- Roman, M. R., Holliday, D. V. and Sanford, L. P. (2001) Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. *Mar. Ecol. Prog. Ser.*, **213**, 215–227.
- Roman, M. R., Zhang, X., McGilliard, C. *et al.* (2005) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnol. Oceanogr.*, **50**, 480–492.
- Roper, D. S. (1986) Occurrence and recruitment of fish larvae in a northern New Zealand estuary. *Estuarine Coastal Mar. Sci.*, **22**, 705–717.
- Sautour, B. and Castel, J. (1995) Comparative spring distribution of zooplankton in three macrotidal European estuaries. *Hydrobiologia*, **311**, 139–151.
- Seuront, L. (2006) Effect of salinity on the swimming behaviour of the estuarine calanoid copepod *Eurytemora affinis*. *J. Plankton Res.*, **28**, 805–813.
- Sindlinger, L. R., Biggs, D. C. and DiMarco, S. F. (2005) Temporal and spatial variability of ADCP backscatter on a continental slope. *Cont. Shelf Res.*, **25**, 259–275.
- Stanton, T. K., Wiebe, P. H., Chu, D. Z. *et al.* (1994) Acoustic characterization and discrimination of marine zooplankton and turbulence. *ICES J. Mar. Sci.*, **51**, 469–479.
- Steffe, A. S. and Pease, B. C. (1988) Diurnal survey of ichthyoplankton abundance, distribution and seasonality in Botany Bay, New South Wales. *Proc. Linn. Soc. N.S.W.*, **110**, 1–10.
- Strydom, N. A., Whitfield, A. K. and Wooldridge, T. H. (2003) The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. *Afr. Zool.*, **38**, 29–43.
- Sutor, M., Cowles, T. J., Peterson, W. T. *et al.* (2005) Comparison of acoustic and net sampling systems to determine patterns in zooplankton distribution. *J. Geophys. Res. Oceans*, **110**, C10S16.
- Thayer, C. W., Hoss, D. E., Kjelson, M. A. *et al.* (1974) Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. *Chesapeake Sci.*, **15**, 9–16.
- Thorne, P. D., Vincent, C. E., Hardcastle, P. J. *et al.* (1991) Measuring suspended sediment concentrations using acoustic backscatter devices. *Mar. Geol.*, **98**, 7–16.
- Valle-Levinson, A., Boicourt, W. C. and Roman, M. R. (2003) On the linkages among density, flow, and bathymetry gradients at the entrance to the Chesapeake Bay. *Estuaries*, **26**, 1437–1449.
- Wade, I. P. and Heywood, K. J. (2001) Acoustic backscatter observations of zooplankton abundance and behaviour and the influence of oceanic fronts in the northeast Atlantic. *Deep-Sea Res. Part II Top. Stud. Oceanogr.*, **48**, 899–924.
- Weeks, A. R., Griffiths, G., Roe, H. *et al.* (1995) The distribution of acoustic backscatter from zooplankton compared with physical structure, phytoplankton and radiance during the spring bloom in the Bellingshausen Sea. *Deep-Sea Res. Part II Top. Stud. Oceanogr.*, **42**, 997–1019.
- Whitfield, A. K. and Harrison, T. D. (1996) *Gilchristella aectuarua* (Pisces: Clupeidae) biomass and consumption of zooplankton in the Sunday Estuary. *South Afr. J. Mar. Sci.*, **17**, 49–53.
- Wiebe, P. H. (1988) Functional regression equations for zooplankton displacement volume, wet weight, dry weight and carbon: a correction. *Fish. Bull.*, **86**, 833–835.
- Witting, D. A., Able, K. W. and Fahay, M. P. (1999) Larval fishes of a Middle Atlantic Bight estuary: assemblage structure and temporal stability. *Can. J. Fish. Aquat. Sci.*, **56**, 222–230.
- Wooldridge, T. H. (1999) Estuarine zooplankton community structure and dynamics. In Allanson, B. R. and Baird, D. (eds), *Estuaries of South Africa*. Cambridge University Press, Cambridge, UK, pp. 470.
- Zimmerman, R. A. and Biggs, D. C. (1999) Patterns of distribution of sound-scattering zooplankton in warm and cold-core eddies in the Gulf of Mexico, from a narrowband acoustic Doppler current profiler survey. *J. Geophys. Res. Oceans*, **104**, 5251–5262.