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

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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 \(24.1 \pm 8.8^\circ C\). Maximum zooplankton (20.5 mgC/m\(^3\)) and fishes (874 larvae/100 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 km², 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 (m³) 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 m³. 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/m³) using the Wiebe equation (Wiebe, 1988):

\[
\log{(DW)} = 0.499 + 0.991 \times \log{(C)} \tag{1}
\]

where \(C\) is the biomass in mgC/m³.

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.
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):

$$S_v = C + 10 \log_{10} \left[ \left( T_x + 273.16 \right) R^2 \right] - L_{DBM} - P_{DBM} + 2aR + K_c (E - E_r)$$

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

Sound absorption coefficient ($a$) was estimated using CTD data recorded at each site and following the equations of Francois and Garrison (Francois and Garrison, 1982a, b).
Values of $S_v$ from the first two depth cells (1–2 m) was omitted due to noise created by the vessel’s hull, whereas $S_v$ from the subsequent 5 m was averaged for comparison with net-derived biomass. Spatio-temporal contour maps of mean $S_v$ were created using SURFER® for the survey area to locate high $S_v$ spots, and examined to ascertain whether they reflected regions of high zooplankton biomass identified from net collections.

**Data analyses**

Replicate biomass samples (mgC/m³) and larval fish concentrations (larvae/100 m³) were averaged and log-transformed (ln) to account for heterogeneity of variance following Cochran’s test. One-way ANOVA was performed to test 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®.

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 (Muyllaert and Sabbe, 1999; Muyllaert et al., 2000; Mouny and Dauphin, 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 ±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 $S_v$. Predictive 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/m³) 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 ($S_v$) can be expressed as $S_v = \log_{10}(\sigma_s/4\pi)$, 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 $S_v = \log_{10}(DW/4\pi)$ (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 (m³/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).
Both zooplankton biomass and larval fish concentrations peaked in November 2001 (13.21 mgC/m$^3$; 207 larvae/100 m$^3$) and again in November 2002 (3.7 mgC/m$^3$; 381 larvae/100 m$^3$), when water temperatures were $\sim$15°C. Lowest mean monthly zooplankton biomass (0.20 mgC/m$^3$) and larval concentrations (0.7 larvae/100 m$^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 mgC/m$^3$) and August 2002 (0.05 mgC/m$^3$). Peaks in zooplankton biomass in the euhaline zone occurred in October 2001 (5.6 mgC/m$^3$) and 2002 (7.11 mgC/m$^3$), whereas peaks in the polyhaline zone occurred in November 2001 (6.7 mgC/m$^3$) and 2002 (5.6 mgC/m$^3$) (Fig. 5a–c). Highest and lowest larval fish concentrations were recorded in the polyhaline zone in November 2002 (874 larvae/100 m$^3$) and June 2001 (0.4 larvae/100 m$^3$), whereas peak larval

![Venice System Salinity zones](image)

**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.

![Temperature (°C) and Freshwater flow (m/s)](image)

**Fig. 3.** Mean (± 95% CI) monthly (a) temperature (°C) along the Tamar Estuary and (b) freshwater flow (m/s) from the North and South Esk rivers between October 2001 and November 2002.
concentrations in the euhaline and meso-oligohaline zones occurred in November 2002 (651 larvae/100 m³) and November 2001 (553 larvae/100 m³) (Fig. 6a–c).

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 ($R = 0.66; r^2 = 0.43; P < 0.001; n = 71$). 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 $\pm 10$ 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/m³), whereas low Sv values ($-80$ to $-75$ dB) match low biomass (0.3–0.5 mgC/m³) 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/m³) and April 2002 (0.7 mgC/m³), whereas

### Table I: Results from one-way ANOVAs (ln-transformed data) for temporal variation of biomass (mgC/m³), and for spatial variation during peak biomass season

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

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.

### Table II: Results from one-way ANOVA (ln-transformed data) for spatial variation of larval fish concentrations (larvae/100 m³) during peak biomass season

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Tukey test</th>
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<tbody>
<tr>
<td>Oct 2001</td>
<td>5.06</td>
<td>2</td>
<td>2.53</td>
<td>3.27</td>
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<tr>
<td>Nov 2001</td>
<td>4.81</td>
<td>2</td>
<td>2.40</td>
<td>3.61</td>
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<tr>
<td>Dec 2001</td>
<td>2.73</td>
<td>2</td>
<td>1.36</td>
<td>2.98</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>Oct 2002</td>
<td>23.50</td>
<td>2</td>
<td>11.75</td>
<td>9.84</td>
<td>**</td>
<td>E P M</td>
</tr>
<tr>
<td>Nov 2002</td>
<td>0.90</td>
<td>1</td>
<td>0.90</td>
<td>0.99</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>

NS, not significant. Tukey test abbreviations: E, euhaline; P, polyhaline; M, meso-oligohaline. **P < 0.01.
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 follow the same spatial distribution with the highest concentration recorded in the polyhaline zone during November 2002 (833 larvae/100 m³) when biomass was only 11 mgC/m³ (Fig. 8b).

**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
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; Beaupre et al., 2003). These include common estuarine-spawning species such as Engraulis australis and P. tasmanianus, and also some gobies (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; Glick 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 ~15°C, match those recorded for zooplankton and larval fishes in late spring in various temperate bays and

| Table III: Stepwise multiple linear regression analysis of biomass variability and environmental factors |
|-------------------------------------------------|-------------------------------------------------|-----------------|-----------------|
| $R = 0.70$ | $\text{adj}R^2 = 0.46$ | $F = 20.4$ | $***$ |
| Temperature | 0.50 | 0.13 | $***$ |
| Freshwater flow | 0.25 | 0.01 | $**$ |
| Salinity | 0.14 | 0.01 | NS |

$\text{adj}R^2$, 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 |
|-------------------------------------------------|-------------------------------------------------|-----------------|-----------------|
| $R = 0.85$ | $\text{adj}R^2 = 0.70$ | $F = 36.8$ | $***$ |
| Temperature | 0.37 | 3.75 | $***$ |
| Zooplankton biomass | 0.26 | 0.71 | ** |
| Freshwater flow | −0.16 | −0.72 | * |
| Salinity | −0.07 | −0.26 | NS |

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

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

![Graph](image-url)
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

Fig. 8. Horizontal contours of mean $S_v$ (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 (mgC/m$^3$, grey circles) and larval fish concentrations (larvae/100 m$^3$, diamonds) have been superimposed at each sampling site. $S_v$ data were not available for the period of May-July 2002 due to instrument malfunction.
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 temporally. 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; Lougee 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-oligohaline zones differing by \(|\Delta Sv| = 10\ dB\). 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 course marine sand in the lower-middle sections (to \(\sim 30\ km\ upstream\)) to small mud particles \(<0.05\ mm\) in the middle-upper sections (to \(\sim 65\ km\ upstream\)), 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 $S_v$ being affected by other factors, such as high upstream sediment concentrations, air bubbles and turbulent currents, our ADCP-measured $S_v$ 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 $S_v$ 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).

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