Estuarine, Coastal and Shelf Science (2000) **50,** 639–654
doi:10.1006/ecss.2000.0591, available online at http://www.idealibrary.com on IDEAL®

Effects of Catchment Activities on Macrofaunal Assemblages in Tasmanian Estuaries

G. J. Edgar[a,c] **and N. S. Barrett**[b]

[a]*School of Zoology, University of Tasmania, GPO Box 252-05, Hobart, Tasmania, 7001 Australia*
[b]*Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Crayfish Point Laboratory, Taroona, Tasmania, 7053 Australia*

Received 23 August 1999 and accepted in revised form 12 January 2000

Silt loadings associated with human activities in catchments were inferred to have an extremely widespread effect on estuarine macrobenthos around Tasmania. Estuaries with human population densities exceeding 10 km^{-2} in catchments consistently possessed muddy rather than sandy beds and shores, and were dominated by infauna rather than epifauna. Estuaries with human population densities below 1 km^{-2} in catchments possessed sandy sediments and numerous epifaunal species. These effects were consistent within groups of estuaries possessing similar hydrology and geomorphology. Although faunal composition differed substantially between estuaries possessing low and high human population densities, the number of macrofaunal species was similar. Population effects therefore could neither be detected using species richness indices, nor by the ABC method. Faunal changes were most clearly detected using disturbance indices weighted by the sensitivity of individual species to human activity. Two such indices, which are based on abundance (DI_n) and productivity (DI_p) data, are suggested to provide useful local indicators of estuarine health.

Keywords: benthos; catchment processes; estuaries; human impacts; macrofauna; siltation; stress; Tasmania

Introduction

Shipping access, availability of dependable fresh water, prevalence of fertile alluvial land, and productivity of waters for fish and shellfish have led worldwide to the concentration of human activity on estuaries. Changes to estuarine ecosystems inevitably follow development as a consequence of factors such as port construction (Whitfield, 1986), channel dredging (van Dolah *et al.*, 1984), introduction of exotic taxa (Carlton, 1989), damming of migration routes (Rosenberg *et al.*, 1995), reduction in freshwater flows (Schlacher & Wooldridge, 1996), siltation (Newcombe & Jensen, 1996), marine farm pollution (Ritz *et al.*, 1989; DeFur & Rader, 1995), and by the direct removal of ecologically-important fish and invertebrate species. Estuaries also provide access to hinterland regions, and serve as conduits for sewage (Cloern, 1996) and fertiliser (Lavery *et al.*, 1991), mine runoff (Winemillter & Morales, 1989), industrial waste (Saiz-Salinas *et al.*, 1996) and heated water (Bamber & Spencer, 1984). The outcome of these activities is often eutrophication (Nixon, 1995; McClelland *et al.*, 1997; Valiela *et al.*, 1997) and macrophyte loss (Silberstein *et al.*, 1986; Boynton *et al.*, 1996), with nearly all estuaries outside polar regions suffering substantial anthropogenic degradation.

While the effects of human activity on estuarine ecosystems have been studied on numerous occasions, most studies have been confined to individual estuaries. More general assessments of the relative intensity of different human impacts at regional, national or international scales have not often been attempted (but see De Jonge *et al.*, 1994). Hence in North America, for example, the question of whether the introduction of exotic species has caused greater disruption to estuarine communities than vegetation clearance remains unanswered. Clearly, the answer in this case will vary greatly between estuaries; however, information on net effects at regional scales is crucial when assessing research priorities. Funding on noticeable human impacts within a few badly-degraded urbanized estuaries may well have occurred at the expense of identifying more subtle impacts affecting estuarine processes throughout large regions.

The aim of the present study was to identify impacts on macrofaunal communities of human activity that extended over a regional scale of ≈1000 km around Tasmania.

---

[c]Tel: +61 3 6226 7632; Fax: +61 3 6226 2745; E-mail: g.edgar@utas.edu.au

0272–7714/00/050639+16 $35.00/0

Methods

Samples of macrofauna retained on a 1 mm sieve were collected using 150 mm diameter corers inserted to a depth of 100 mm at 55 sites in 48 estuaries distributed around Tasmania and associated Bass Strait islands, as described in more detail in Edgar *et al.* (2000). Sites were selected haphazardly from the universe of estuarine sites around the coast and encompassed a wide range of environmental conditions, with salinities varying from 0 to 53, tidal range varying from 0 to 2·3 m, and estuary catchment area varying from 6 to 13 100 km^2. At each site, cores were collected using a spatially-nested sampling design based on (i) three random transect lines perpendicular to the shore ≈100 m apart, (ii) three to five fixed tidal heights down each transect (high water mark, mid tide level, low water mark, 0·3 m below low water, 0·7 m below low water), and (iii) two random replicates ≈1 m apart at each height down each transect.

In the laboratory, samples were sorted into size-classes using a nested series of sieves. The biomass of each animal >2 mm sieve size was directly determined or estimated from length data and length/weight regressions. The biomass of animals <2 mm sieve size was estimated using general data on the mean biomass of animals associated with each sieve, as described in Edgar (1990). Estimates of the daily productivity of benthic invertebrates were calculated using biomass estimates for each animal and the equation $\mathrm{P}=0{\cdot}0049{\star}\mathrm{B}^{0{\cdot}80}\mathrm{T}^{0{\cdot}89}$, which relates daily macrobenthic productivity P ($\mu\mathrm{g\ d}^{-1}$) to ash-free dry weight B (μg) and water temperature T (°C) (Edgar, 1990). Data collected in replicate samples from each site were amalgamated in the present study, with the mean density value for each species at each site used in analyses (Edgar *et al.*, 1999).

Biological relationships between sites were assessed using non-metric multidimensional scaling (MDS), as run by the PRIMER program (Carr, 1996). The similarity matrices used in MDS were calculated between paired sites using the Bray-Curtis similarity coefficient after double root transformation, as recommended by Faith *et al.* (1987) and Clarke (1993). The usefulness of the MDS display of relationships between sites is indicated by the stress statistic, which if <0·1 indicates that the depiction of relationships is good, and if >0·2 that the depiction is poor (Clarke, 1993).

The density of individual species at the different sites was related to human activity using Spearman rank correlation coefficients. Species with high correlation values were positively associated with human activity while species with low values were negatively associated. Human activity was quantified using two indices, the human population density and percent cleared land in catchment. In order to weight these two indices for activity in the immediate vicinity of the estuary, data for each site were calculated as the mean of the value for the total catchment area and the value for the estuarine drainage area. The estuarine drainage area was defined as that region draining directly into the estuary rather than into the major associated river. The latter, in turn, was defined as occurring upstream of the point on 1:100 000 topographic maps where river banks were shown as separate lines, where the 10 m contour line crossed the river flow line, or where probable obstructions to tidal flow such as gorges were shown on maps (see Edgar *et al.*, 2000).

Data on human population density and percent cleared land in catchments were obtained by overlaying GIS maps of catchment areas on digital population census and land use data sets (see Edgar *et al.*, 1999, 2000), following methods more fully described by Graddon (1997). Data on catchment land use were obtained by categorization of satellite images of the Tasmanian mainland, but were not available for estuaries on Bass Strait islands. Data on total annual runoff into estuaries were obtained by calibrating a GIS rainfall prediction model based on flow data from 63 gauged rivers and 504 rainfall stations (Edgar *et al.*, 2000), while salinity, tidal range and the silt/clay content of sediments associated with each site were recorded in the field. Salinity was measured at 0·1 m depth below the surface during low tide, tidal range was estimated as the distance between the high tide layer of deposited flotsam and maximum retreat of water on the day of sampling, and the silt/clay (<63 μm) particle fraction was determined for aggregated sediments collected in shallow subtidal (0·3–0·7 m) depths. The latter variable was assessed at only 39 of the 55 sites sampled for macrobenthos.

Spearman rank correlation coefficients (R_s) relating animal abundance and human activity for all invertebrate species across the 55 sites were used to calculate an index of anthropogenic disturbance (*DI*) for each site:

$$DI_n = \mathrm{E}R_{s_i} \star n_i / N$$

where n_i is the abundance of species i and N is total abundance of all species at the site. This index was calculated so that estuarine assemblages at Tasmanian sites could be categorized with respect to human impact using a single univariate value. The index eliminated much of the largely irrelevant information associated with each site that was caused by variation in natural environmental factors such as salinity and tidal range rather than human impact, as well as ‘ noise ’ contributed by species that occurred at a wide range of sites but were not greatly influenced by human activity. Such an index was considered a potentially useful tool when monitoring changes to impacted habitats over time, and for assessing the spatial scale of impacts.

Comparable disturbance indices were also calculated using data on the estimated productivity and biomass of macrofauna at each site ($DI_p = \mathrm{E}R_{s_i} \star p_i / P$ and $DI_b = \mathrm{E}R_{s_i} \star b_i / B$, where p_i and b_i represent total productivity and biomass of species i, and P and B represent total productivity and biomass of all macrofauna at the site).

Assessment of *DI* in the present study was partly confounded by circularity of calculations, in that indices were calculated using information on relationships between species abundance and disturbance to estuaries (population density), and then tested using aggregated site information against the same population density variable. Ideally, derivation and assessment data sets should have been independent because any variable will show a relatively high correlation with *DI* when used also to calculate the weightings for each species that form the basis of *DI*. To assess the scale of this bias, weightings for species were calculated using a dummy variable composed to random numbers, and then the correlation coefficient between *DI* and the original dummy variable calculated. The Abundance/Biomass Comparison (ABC) method of Warwick (1986) was also applied to the macrofaunal data set to assess whether this procedure has value in identifying sites subjected to human disturbance. In this procedure, the cumulative abundance and biomass of species ranked in order to importance in a sample were graphically compared for samples collected at four sites in estuaries with highest and lowest population densities in catchments. Only samples collected at or below low water mark were used in this analysis. Samples from higher tidal levels were excluded because they tended to be influenced by terrestrial as well as estuarine processes (Edgar & Barrett, unpublished data). Patterns of variation in the fauna were highly consistent between 0·3 and 0·7 m depth at sites examined. The hypothesis tested using the ABC procedure was that anthropogenic impact causes elevated densities of small individuals, hence total abundance is dominated by relatively few species compared to biomass under disturbed conditions (Warwick *et al*., 1987).

Results

Relationships between species abundance and human activity

Macrofaunal relationships between sites are depicted using MDS in Figure 1. The plot shown is three-dimensional because the equivalent two-dimensional plot produced a relatively poor description of the data (stress=0·12 cf. 0·17). The bubble plot overlay of human population density in catchment indicates that faunal assemblages varied between sites in a pattern related to population density (Figure 1). This correspondence occurred almost exclusively along MDS axis 1. The site with negligible population density at the extreme right of axis 1 was the Wanderer Estuary, an aberrant location with extremely low faunal productivity and little similarity to any other site (Edgar *et al*., 1999). Percentage cleared land in catchment and silt-clay content of sediments at the sample site showed relatively poor relationships with macrofaunal assemblages.

Relationships between densities of species at sites and the level of anthropogenic disturbance, as assessed using Spearman rank correlation coefficients that relate total animal abundance at each site with human population density and percent cleared land, are listed for abundant species in Table 1. Significance values have not been assigned to correlation coefficients because of uncertainty caused by the large number of species investigated during the study increasing the probability of Type I error, and the generally small number of sites at which each species was recorded affecting the probability of Type II error. A total of 157 of the 390 taxa collected were recorded at a single site only, with the great majority of these animals considered marine vagrants (Edgar *et al*., 1999).

Population density was generally more highly correlated with species abundance than percent cleared land, and therefore appeared to be the better discriminator of human impacts. Population density produced a highest correlation coefficient of 0·51 for *Tellina deltoidalis* and a minimum value of −0·45 for *Limnoporeia kingi*, compared to maximum and minimum values amongst all species of 0·37 and −0·29 using percent cleared land data.

The six widespread species most highly correlated with human population density (Table 1) were infaunal species typically associated with mudflats. Other species that were also highly correlated with population density but not shown in Table 1 because they occurred at less than 12 sites, and so have a high chance of being spuriously correlated, were also

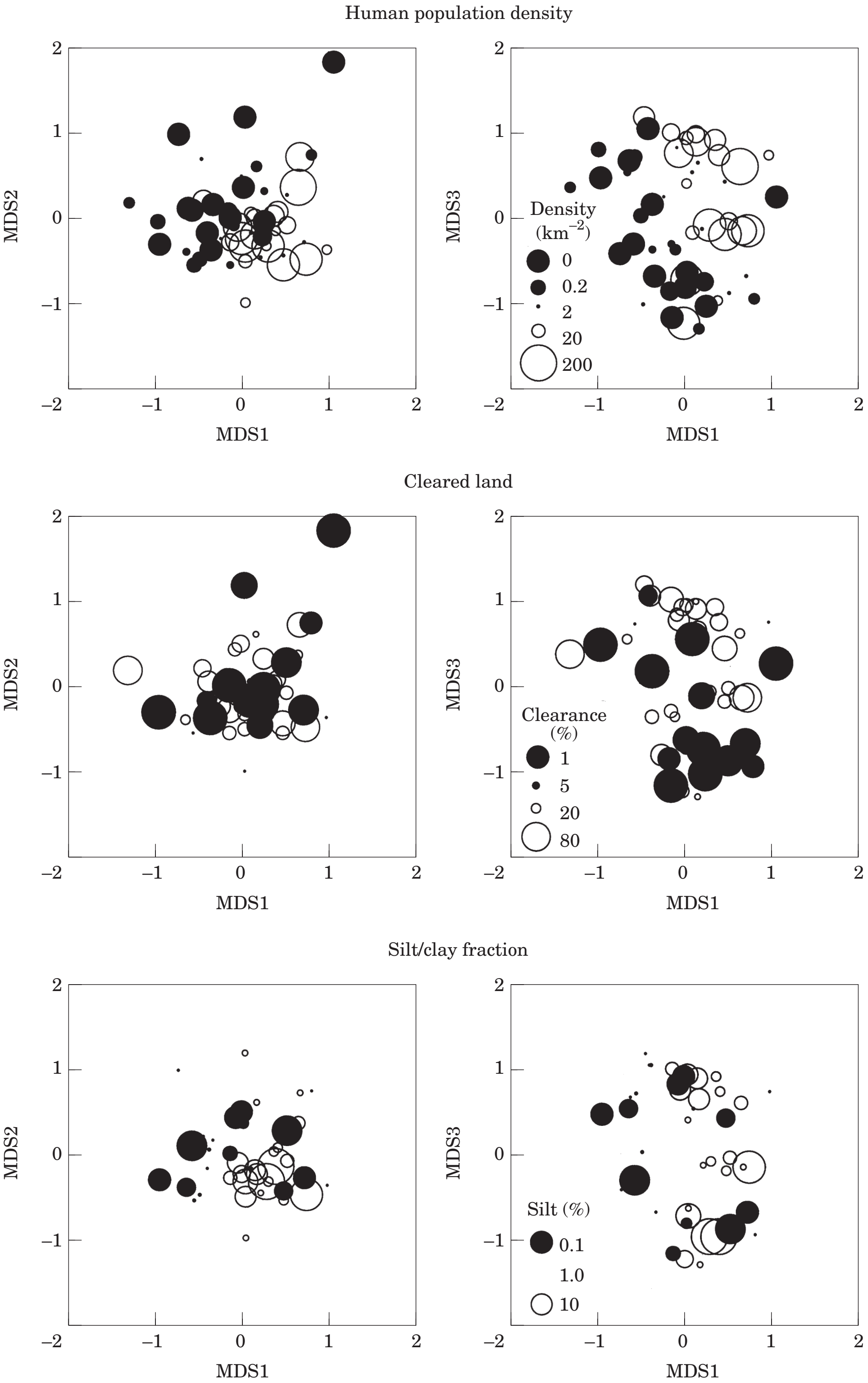


FIGURE 1. Bubble plot overlays of human population density in catchment, percentage cleared land in catchment and percentage of silt and clay (<63 µm) in sediments on 3-d MDS depiction of faunal relationships between sites. Note that MDS axes values provide an arbitrary frame of reference.

TABLE 1. Spearman rank correlation coefficients (R_s) relating abundance at different sites of widespread species (i.e. the 46 species present at 12 or more sites) with population density (Pop) and % cleared land (Clear). Infaunal or epifaunal habit of species is also shown

Species	Habit	Group	Pop R_s	Clear R_s
Tellina deltoidalis	Infaunal	Bivalve	0·51	0·37
Magelona sp.	Infaunal	Polychaete	0·39	0·30
Lumbrineris sp. 1	Infaunal	Polychaete	0·39	0·35
Macrophthalmus latifrons	Infaunal	Crab	0·36	0·24
Nephtys australiensis	Infaunal	Polychaete	0·32	0·15
Callianassa arenosa	Infaunal	Shrimp	0·30	0·17
Nassarius burchardi	Epifaunal	Gastropod	0·26	0·15
Neanthes vaalii	Infaunal	Polychaete	0·24	0·26
Paragrapsus gaimardii	Epifaunal	Crab	0·22	0·19
Gammaropsis sp. 1	Epifaunal	Amphipod	0·21	0·01
Actaecia bipleura	Epifaunal	Isopod	0·19	0·27
Phyllodoce sp.	Epifaunal	Polychaete	0·19	0·35
Limnoporeia yarrague	Epifaunal	Amphipod	0·18	0·22
Australonereis ehlersi	Infaunal	Polychaete	0·13	0·02
Dimorphostylis colefaxi	Epifaunal	Cumacean	0·09	− 0·04
Heteromastus sp.	Infaunal	Polychaete	0·08	0·11
Mictyris platycheles	Infaunal	Crab	0·07	0·14
Exoediceroides ?maculosus	Infaunal	Amphipod	0·07	0
Nassarius pauperatus	Epifaunal	Gastropod	0·07	− 0·08
Mysella donaciformis	Infaunal	Bivalve	0·07	0·10
Paracorophium cf excavatum	Infaunal	Amphipod	0·06	0·20
Macrobrachium sp.	Epifaunal	Shrimp	0·06	− 0·09
Pseudolana concinna	Epifaunal	Isopod	− 0·01	− 0·17
Xenostrobus inconstans	Epifaunal	Bivalve	− 0·04	0·02
Paracalliope australis	Epifaunal	Amphipod	− 0·05	0·17
Nemertean sp. 1	Infaunal	Nemertean	− 0·06	− 0·05
Melita sp.	Epifaunal	Amphipod	− 0·07	0·20
Arthritica semen	Infaunal	Bivalve	− 0·11	0·01
Euzonus sp.	Infaunal	Polychaete	− 0·11	0·05
Katelysia scalarina	Infaunal	Bivalve	− 0·11	0·03
Capitella sp. 2	Infaunal	Polychaete	− 0·12	0
Tatea rufilabrus	Epifaunal	Gastropod	− 0·12	0·02
Leitoscoloplos normalis	Infaunal	Polychaete	− 0·12	− 0·15
Boccardiella sp.	Infaunal	Polychaete	− 0·13	0·09
Salinator fragilis	Epifaunal	Gastropod	− 0·14	− 0·12
Simplisetia aequisetis	Infaunal	Polychaete	− 0·15	− 0·25
Perinereis vallata	Infaunal	Polychaete	− 0·19	0·04
Chironomid spp.	Epifaunal	Insect	− 0·20	0·01
Zeacumantus diemenensis	Epifaunal	Gastropod	− 0·21	0·09
?Mysella sp.	Infaunal	Bivalve	− 0·24	− 0·10
Ascorhis victoriae	Epifaunal	Gastropod	− 0·27	− 0·23
Exosphaeroma sp.	Epifaunal	Isopod	− 0·28	− 0·22
Hydrococcus brazieri	Epifaunal	Gastropod	− 0·28	0
Amarinus lacustris	Epifaunal	Crab	− 0·35	− 0·21
Eubittium lawleyanum	Epifaunal	Gastropod	− 0·38	− 0·29
Limnoporeia kingi	Epifaunal	Amphipod	− 0·45	− 0·17

mudflat dwelling species (e.g. the bivalve *Notospisula trigonella*—R_s=0·40 and the crabs *Heloecius cordiformis*—R_s=0·28 and *Helograpsus haswellianus*—R_s=0·24). By contrast, the six widespread species showing strongest negative correlations with population density were epifaunal species. This included three species that generally associate with sandflats in similar salinity and tidal height conditions to the mudflat species (*Eubittium lawleyanum*, *Hydrococcus brazieri* and *Exosphaeroma* sp.). Most additional species with strong negative correlations with population density that were not included in Table 1 because of restricted distribution were also sandflat inhabitants (e.g. the bivalve *Wallucina assimilis*—R_s= − 0·32 and

TABLE 2. Disturbance index values calculated using abundance (DI_n), biomass (DI_b) and productivity (DI_p) data. DI_n was also calculated using a reduced 30 species data set and using percent cleared land rather than human population density as the initial correlate. DI indices have been rescaled for comparisons in the range from 0 to 10 (where 0 indicates the site examined during the study with lowest DI and 10 the site with highest DI). Human population density and percent cleared land in catchment are also shown. Land clearance data were not available for seven estuaries on Bass Strait islands

Estuary	Date	DI_n	DI_b	DI_p	DI_n Reduced	DI_n % Cleared	Population	% Cleared
Sea Elephant	24 Feb 97	1·09	5·90	0·39	2·09	9·38	0·23	—
Yellow Rock	23 Feb 97	0·85	0	0·78	2·12	10·00	1·20	—
North East Inlet	8 May 97	2·41	5·34	1·34	2·64	4·50	0·12	—
Patriarch Inlet	9 May 97	2·26	5·82	1·88	1·72	4·24	0·06	—
Cameron Inlet	9 May 97	2·43	2·26	1·33	1·95	4·97	0·12	—
Modder	12 May 97	4·03	4·22	2·64	1·77	6·69	0	—
Rices	6 May 97	0	3·90	0·19	1·23	6·48	0	—
Welcome Inlet	21 Feb 97	0·01	2·64	2·01	2·01	4·23	0·57	22·0
Mosquito Inlet	22 Feb 97	3·11	5·78	1·23	2·52	2·86	0	1·43
East Inlet	15 Jan 97	2·78	7·80	2·23	2·55	2·69	7·61	49·2
Black/Dip	14 Jan 97	7·44	7·42	5·71	7·06	3·26	1·78	33·2
Detention	13 Jan 97	5·69	6·88	4·54	9·15	2·26	3·86	33·3
Cam	26 Sep 96	5·89	8·28	5·36	8·08	5·49	74·4	53·8
Blythe	16 Jan 97	6·02	9·21	7·63	8·99	4·72	25·7	28·2
Leven	25 Sep 96	7·14	5·62	3·36	9·95	1·24	71·6	45·6
Leven	17 May 97	7·37	3·91	3·84	9·39	1·44	71·6	45·6
Don	24 Sep 96	5·84	10·00	7·46	8·73	4·79	152·0	69·8
Port Sorell	17 Jan 97	6·23	0·69	3·14	8·77	1·97	11·9	31·2
Tamar/Low Head	16 Dec 96	6·14	5·55	4·83	8·17	3·05	39·8	36·00
Tamar/Paper Beach	17 Dec 96	9·15	7·08	10·00	9·91	0	39·8	36·00
Tamar/Paper Beach	17 Jun 97	10·00	5·70	9·86	10·00	0·13	39·8	36·00
Pipers	20 Nov 96	5·53	7·00	4·55	7·67	2·85	3·21	28·7
Tomahawk	22 Nov 96	4·30	7·14	3·09	7·40	5·25	0·63	52·5
Boobyalla	19 Nov 96	4·81	7·29	5·14	2·27	5·59	1·16	41·1
Little Musselroe Bay	14 Nov 96	1·26	4·05	0·33	1·12	3·12	0·39	72·7
Ansons Bay	12 Nov 96	4·93	6·52	3·28	4·34	4·40	2·82	8·21
Big Lagoon	13 Nov 96	2·46	5·95	1·64	2·06	8·86	0·14	1·28
Georges Bay	11 Nov 96	6·40	3·92	6·83	9·64	3·17	17·7	15·6
Hendersons Lagoon	13 Nov 96	3·14	6·01	4·87	6·81	6·06	1·04	25·7
Bryans Lagoon	13 May 97	1·36	2·04	0·79	2·10	9·48	0	0
Great Swanport	23 Dec 96	2·62	5·44	2·24	2·87	7·39	0·43	22·8
Lisdillon	17 Sep 96	2·68	0	4·14	2·41	7·31	3·66	42·9
Prosser	16 Sep 96	5·17	6·41	6·13	5·65	6·06	10·3	17·8
Earlham Lagoon	20 Aug 96	1·06	2·37	2·90	1·05	6·13	0·42	28·2
Pittwater	23 Oct 96	3·57	2·93	4·17	4·42	2·78	26·5	55·8
Derwent/Cornelian Bay	24 Apr 96	6·97	9·06	7·23	8·35	5·22	164·0	30·3
Derwent/Cornelian Bay	13 Feb 97	7·20	8·64	7·38	8·33	4·18	164·0	30·3
Derwent/Bridgewater	21 Oct 96	7·18	3·87	6·22	2·17	6·31	164·0	30·3
Derwent/Claremont	21 Oct 96	5·58	6·21	4·63	5·45	6·46	164·0	30·3
Browns	2 Jul 96	6·16	9·04	7·90	9·32	2·98	279·0	21·0
Huon/Eggs and Bacon	6 Nov 96	7·33	5·14	3·69	8·39	4·90	7·92	12·2
Huon/Brabazon	5 Nov 96	6·37	5·46	5·35	9·04	3·55	7·92	12·2
Huon/Cradoc	31 Oct 96	5·74	5·76	4·68	7·79	6·82	7·92	12·2
Huon/Cradoc	16 May 97	5·82	7·03	5·27	5·76	6·75	7·92	12·2
Hastings	9 Jan 97	5·66	6·61	4·78	9·02	5·64	0·95	0·57
Southport Lagoon	19 Jun 97	0·05	2·82	0·15	1·58	5·06	0	0
Cloudy Bay/southwest	18 May 97	1·22	2·07	1·85	2·52	6·17	0·32	10·7
Cloudy Bay/northeast	24 May 97	0·84	4·68	1·92	2·36	5·22	0·32	10·7
Cockle Creek	7 Jan 97	7·40	6·60	3·39	7·53	2·38	1·73	0
New River Lagoon	18 Feb 97	2·42	0·51	0·93	2·08	8·88	0	0
Bathurst Harbour	19 Feb 97	3·48	8·61	2·72	7·33	8·21	0·03	0
Payne Bay	19 Feb 97	0·72	1·93	1·86	2·06	5·24	0	0
Wanderer	20 Feb 97	6·70	8·49	5·77	5·26	1·66	0	0

TABLE 2. (*Continued*)

Estuary	Date	DI_n	DI_b	DI_p	DI_n Reduced	DI_n % Cleared	Population	% Cleared
Macquarie/heads	30 Sep 96	5·38	7·30	4·50	5·26	4·78	2·94	0·31
Macquarie/Swan Basin	23 Jun 97	3·66	2·07	1·58	1·74	6·81	2·94	0·31
Henty	25 Jun 97	1·07	0·03	0	5·26	9·10	0·07	0·19
Pieman	24 Jun 97	4·50	3·28	2·75	0	5·85	0·53	0·96
Nelson Bay	14 Jan 97	3·44	2·03	1·65	0·71	6·15	0	0·64
Arthur	13 Jan 97	3·81	2·39	2·54	1·98	7·51	0·31	17·3

the gastropods *Diala suturalis*—$R_s = -0{\cdot}25$ and *Haminoea maugensis*—$R_s = -0{\cdot}24$).

Calculation of the disturbance index DI_n for each site using Spearman rank correlation coefficients and abundance data indicated a wide range of values between sites. The site with the highest *DI*, and therefore the one most dominated by species typical of disturbed (i.e. heavily populated) conditions, was Paper Beach (Tamar Estuary) while Rices River was found to be the least disturbed. DI_n values for all sites sampled are listed in Table 2.

DI_n appears useful as an environmental indicator of anthropogenic disturbance of sites. It retains a high correlation with population density ($R_s = 0{\cdot}74$) and, to a lesser extent, with percent cleared land ($R_s = 0{\cdot}55$), but was not strongly correlated with the major physical variable salinity ($R_s = -0{\cdot}31$). In addition, bubble plots overlaying DI_n values on MDS results showed a very good separation of sites (Figure 2), particularly for the plot of MDS axis 1 *vs* axis 3. DI_n therefore has a high degree of faunal consistency and discriminates well between sites.

Disturbance indices based on reduced species data

In order to determine whether calculations of DI_n were dominated by a limited number of influential species, this index was recalculated using data from the 15 species most highly positively and negatively correlated with human population density, as listed in Table 3.

Correlation of *DI* values with human population density for sites calculated using the reduced species data set was similar to that for the full data set ($R_s = 0{\cdot}73$ cf. 0·74), hence little information had been lost. The bubble plots of *DI* overlaying MDS results were also similar to plots obtained using all species (Figure 2).

Disturbance indices based on biomass and productivity data

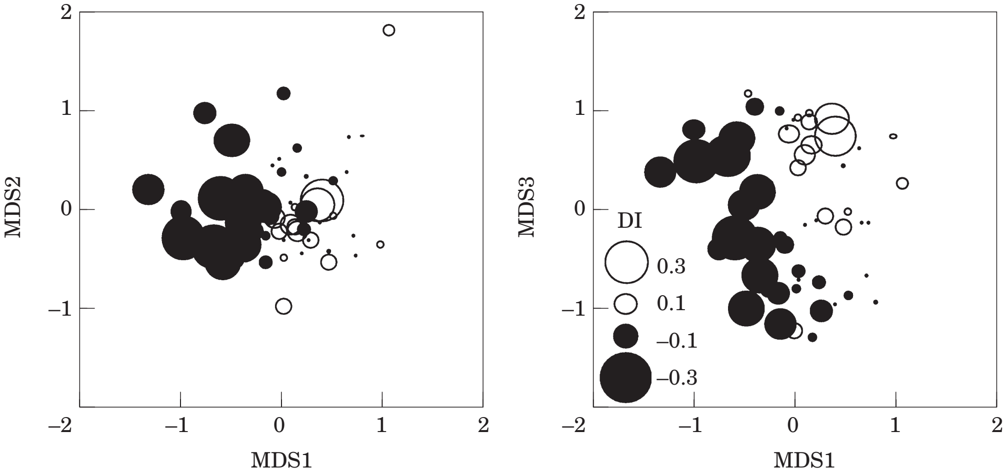
DI was also calculated using data on the total biomass (DI_b) and estimated productivity (DI_p) of species at each site rather than total numbers (DI_n). The bubble plot overlays on MDS results (Figure 3) indicated that sites separated less strongly on the basis of DI_b than on DI_p or DI_n. Relatively few sites possessed high DI_p values (Table 2).

DI_n and DI_p both showed very little change over time, with DI_p marginally more stable (see Table 2, where *DI* values for sites sampled on two occasions are shown). By contrast, DI_b fluctuated considerably between sampling occasions, depending partly on the occasional collection of very large individuals. After *DI* was rescaled to range between 0 and 10, the average standard deviation at sites between times was 0·84 for DI_b compared with 0·25 and 0·24 for DI_n and DI_p respectively.

DI_p was the best performing of all indices examined in terms of retaining its correlation with human population density ($R_s = 0{\cdot}78$, Table 4), while the correlation of DI_b was relatively poor ($R_s = 0{\cdot}40$). DI_p also maintained a better correlation with the other disturbance variable, percent cleared land, than DI_n and was less influenced by the major physical variables salinity, tidal range and total annual runoff (Table 4). DI_p maintained a high correlation with the silt/clay fraction of sediments, tidal range and total annual runoff. This, given the high correlation of population density itself with these variables, was expected. DI_n, DI_b and DI_p were all moderately negatively correlated ($-0{\cdot}49 < R_s < -0{\cdot}28$) with the density of animals at sites but were not greatly affected by the total biomass, total estimated productivity or total number of species.

Assessment of *DI* using species weightings calculated for a dummy variable composed of random

Full data set



Reduced data set

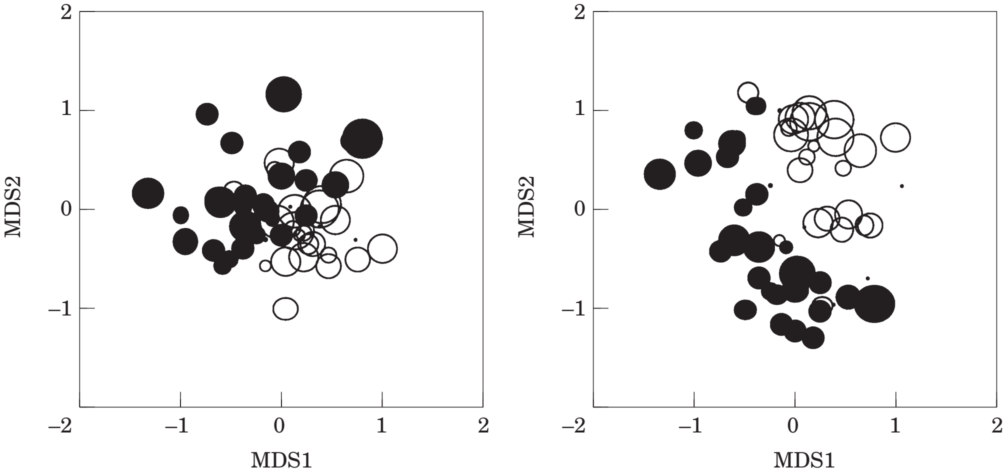


FIGURE 2. Bubble plot overlays of DI_n values on 3-D MDS depiction of faunal relationships between sites. Analyses based on full faunal data set and reduced 30 species data set are shown.

numbers, and then back correlated against *DI*, produced a mean correlation coefficient of 0·49 for 50 dummy variables. This value was slightly higher than the correlation coefficient relating percent cleared land in catchment with the DI_n values calculated using that variable (=0·44, Table 4) and the correlation coefficient for DI_b and population density (=0·40, Table 4). *DI* calculated using percent cleared land and DI_b therefore both possessed negligible relationship with the biota.

By contrast, comparable correlation coefficients based on human population density data were very high for both DI_n (R_s=0·74) and DI_p (R_s=0·78). In terms of the proportion of total variance explained (R^2), statistical bias assessed using dummy variables explained 24% (=$0{\cdot}49^2$), leaving 31% (=$0{\cdot}74^2$–$0{\cdot}49^2$) and 37% (=$0{\cdot}78^2$–$0{\cdot}49^2$) of the remaining 76% attributable to population density for DI_n and DI_p, respectively. After correction for circularity in calculations, the correlation coefficients between DI and human population density therefore remained high at 0·64 (=√(0·31/0·76)) and 0·70 (=√(0·37/0·76)) for DI_n and DI_p, respectively.

Effects of estuary type

Because *DI* values and human population density were both highly correlated with other environmental variables, the possibility that the strong relationship between *DI* and population density was driven primarily by covariation with environmental factors rather than a direct relationship was examined by partitioning estuaries on the basis of geomorphological and hydrological type. Tasmanian estuaries were

TABLE 3. Spearman rank correlation coefficients (R_s) relating human population density in catchments with total abundance of animals for 15 species showing highest and lowest correlations

Species	r_s	Species	r_s
Tellina deltoidalis	0·51	*Limnoporeia kingi*	− 0·45
Notospisula trigonella	0·40	*Eubittium lawleyanum*	− 0·38
Magelona sp.	0·39	*Amarinus lacustris*	− 0·35
Lumbrineris sp. 1	0·39	*Wallucina assimilis*	− 0·32
Macrophthalmus latifrons	0·36	*Scolecolepides* sp.	− 0·31
Nephtys australiensis	0·32	*Hydrococcus brazieri*	− 0·28
Callianassa arenosa	0·30	*Exosphaeroma* sp.	− 0·28
Barantolla lepte	0·30	*Olganereis edmonsi*	− 0·27
Heloecius cordiformis	0·28	*Ascorhis victoriae*	− 0·27
Corophium sp.	0·27	Glycerid sp. 1	− 0·25
Nassarius burchardi	0·26	*Diala suturalis*	− 0·25
Placamen placida	0·25	*Solemya* sp.	− 0·24
Glycerid sp. 2	0·25	*?Mysella* sp.	− 0·24
Helograpsus haswellianus	0·24	*Haminoea maugensis*	− 0·24
Neanthes vaalii	0·24	*Cyamiomacra mactroides*	− 0·22

subdivided in an associated study (Edgar *et al.*, 2000) into nine groups on the basis of biologically-important environmental characteristics (viz., presence of a seaward barrier, tidal range, salinity, estuary size and river runoff), with six of these estuary groups investigated for macrofauna at more than three sites. Relationships between *DI* and human population density within these six estuary categories (barred low-salinity estuary, open polyhaline estuary, marine inlet, mesotidal river estuary, microtidal drowned river valley and open microtidal river estuary) were investigated using Analysis of Covariance (ANCOVA). Results based on *DI* as dependent variable, population density as independent variable (log $x+0{\cdot}1$), and estuary type as grouping variable are presented in Table 5.

None of the three *DI* indices showed a significant interaction between estuary type and log population density (analysis with interaction in Table 5), hence the slopes of the regression equations in different estuary types were similar and the interaction variable was removed from the second analysis. DI_n and DI_p both showed extremely strong relationships with population density after the effects of estuary were taken into account (analysis without interaction in Table 5, $P<0{\cdot}001$); however, DI_b possessed no significant relationship with population density but a significant relationship with estuary type. The overall significant relationship between DI_b and population density resulted from different estuary types possessing differing mean levels of DI_b, and population density also differing significantly between the estuary types.

When comparable ANCOVAs were conducted using four other important environmental variables (tidal range, log total annual runoff, salinity and log silt/clay content of sediments) in place of human population density, no significant ($\alpha=0{\cdot}05$) interactions were detected, hence slopes were also considered homogenous in these ANCOVAs. Salinity and log total annual runoff were found to vary significantly with *DI* once the effects of different estuary types were taken into account (Table 6), although significant variation in *DI* occurred between estuaries of different types. DI_n varied significantly with tidal range within different estuary groups, while DI_n and DI_p also varied with the percentage silt/clay content of sediments.

Relationships between DI_n, human population density in catchment, silt/clay content of sediments and estuary groups are shown as scatterplots in Figure 4. These relationships were non-linear, with negligible change in both *DI* and the silt/clay content of sediments occurring for sites with population densities between 0 and 1 km^{-2}, rapid increases in dependent variables occurring when densities were between 1 and 10 km^{-2}, and then little difference between sites in catchments with densities >10 km^{-2}.

Abundance/biomass comparisons

Results of Warwick's (1986) ABC procedure for sites in estuaries with highest human population densities and sites lacking population within catchments are shown in Figure 5. Biomass curves lacked any consistent pattern in relation to abundance curves, rather than showing greater elevation at undisturbed sites, as

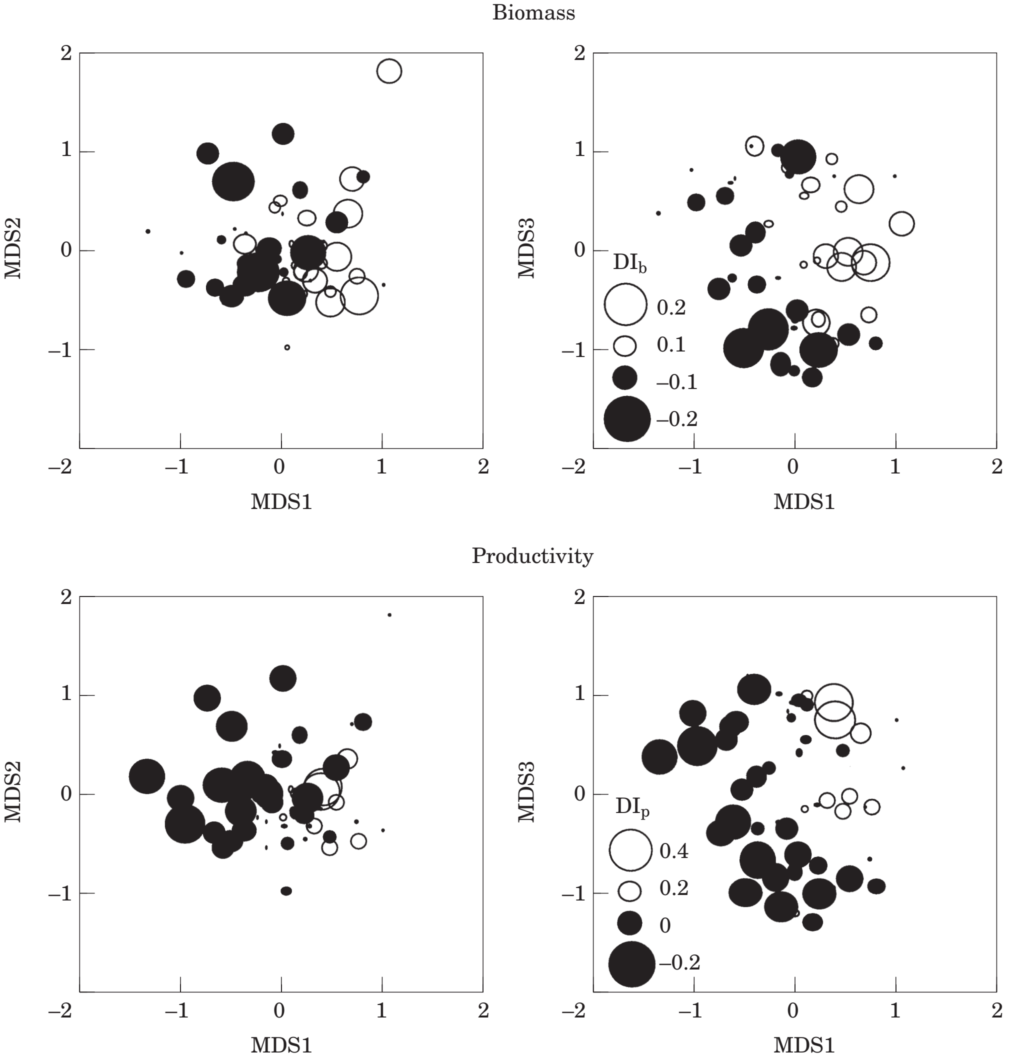


FIGURE 3. Bubble plot overlays of DI_b values calculated using biomass data and DI_p values calculated using estimated productivity data on MDS results.

would be expected if anthropogenic impact caused high densities of small species. The only noticeable trend in the complete data set, which includes sites not shown in Figure 5, related to the salinity of sites. Marine sites (e.g. Kelly Basin) were often dominated in terms of biomass by a few relatively large bivalves, while freshwater-influenced sites were generally inhabited by dense populations of small amphipods and hydrobiid gastropods.

Discussion

Biological indicators of human disturbance

The two anthropogenic disturbance indices proposed in this study, DI_n and DI_p, appear to be sensitive biological indicators of human impacts within Tasmanian estuaries. Both indices were highly correlated with human population density within the catchment area, discriminated between sites with different faunal characteristics (Figure 2), and showed negligible change between different seasons. While these indices should prove useful for monitoring biological changes in Tasmanian estuaries over time, they have restricted geographic applicability because of their basis on correlation coefficients for individual species.

The index based on faunal abundance, DI_n, has a single major advantage over the index based on faunal productivity, DI_n, in that it is relatively simple to measure and comprehend. The advantage of DI_p over DI_n is that it is more biologically meaningful because DI_p is not heavily biased by either large- or small-sized

TABLE 4. Spearman rank correlation coefficients relating disturbance indices calculated using abundance (DI_n), biomass (DI_b) and productivity (DI_p) data, human population density and environmental variables. In addition to the full data set, DI_n was calculated using a reduced 30 species data set and using percent cleared land rather than human population density as the initial correlate

Variable	DI_n	DI_b	DI_p	DI_n Reduced	DI_n % Cleared	Population
Population density	0·74	0·40	0·78	0·73	0·41	1·00
% Cleared land	0·37	0·28	0·46	0·43	0·44	0·67
Salinity	−0·30	−0·13	−0·26	−0·11	0·31	−0·21
Tidal range	0·50	0·38	0·47	0·59	0·61	0·57
Latitude	−0·18	−0·02	−0·24	−0·20	0·17	−0·16
Total annual runoff	0·52	0·12	0·47	0·35	0·10	0·49
% Silt/clay	0·59	0·29	0·60	0·45	0·18	0·65
Species number	−0·10	−0·15	−0·02	0·13	0·36	0·11
Faunal density	−0·49	−0·28	−0·38	−0·55	−0·53	−0·26
Faunal biomass	−0·04	−0·09	−0·05	0·12	0·40	0·14
Faunal productivity	−0·08	−0·15	−0·11	0·04	0·28	0·12

TABLE 5. Results of Analyses of Covariance investigating the relationship between *DI* calculated using abundance, biomass and productivity data and log-transformed human population density in catchments associated with estuaries grouped into six geomorphological and hydrological types

		Abundance (DI_n)			Biomass (DI_b)			Productivity DI_p)		
Effect	DF	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Analysis with interaction										
Estuary	5	8·854	5·026	0·001	11·293	2·782	0·030	2·553	1·619	0·177
Population	1	14·149	8·032	0·007	4·747	1·169	0·286	26·291	16·668	<0·001
Population × estuary	5	4·005	2·273	0·065	4·872	1·200	0·326	1·056	0·669	0·649
Error	41	1·762			4·059			1·577		
Analysis without interaction										
Estuary	5	5·803	2·894	0·024	19·259	4·644	0·002	3·400	2·236	0·067
Population	1	53·615	26·735	<0·001	3·508	0·846	0·363	71·345	46·919	<0·001
Error	46	2·005			4·147			1·521		

species (Edgar, 1990; Edgar & Shaw, 1995; Warwick & Clarke, 1993). Also, the productivity of a species is approximately proportional to total food consumption, total respiration and total reproductive output of that species, and so provides a relative index of its trophic importance (Edgar, 1993). By contrast, indices which relate the abundance of a species to others have much less biological meaning because they can be influenced by one or two species of small size that contribute relatively little to the functioning of the community. Small species tend to be far more abundant in samples than large species.

An additional advantage of DI_p over DI_n was that it showed a higher correlation with percent cleared land, and so possibly responded to a wider range of human impacts (Table 4). DI_p was also less strongly correlated with natural environmental variables (salinity, tidal range, total annual runoff) and the total animal density of samples ($r_s = -0{\cdot}38$ cf. $-0{\cdot}49$).

The extent to which DI_n and DI_p are affected by natural physical factors and total sample size needs to be clarified in future studies. This is best done by manipulation of the level of anthropogenic impact independently of changes in physical factors. Such studies should also examine whether the biological indicators are affected by a large or narrow range of anthropogenic impacts, including siltation, nutrification, reduced oxygen concentrations and heavy metal concentrations.

Widespread human impacts in estuaries are likely to prove difficult to detect using methods other than disturbance indices, given that human impacts are often less obvious than pronounced relationships with natural environmental variables such as salinity (see

TABLE 6. Results of ANCOVAs relating DI calculated using abundance, biomass and productivity data to environmental variables (tidal range, log total annual runoff, salinity and log %silt/clay content of sediments) for estuaries grouped into six geomorphological and hydrological types

		Abundance (DI_n)			Biomass (DI_b)			Productivity (DI_p)		
Effect	DF	MS	F	P	MS	F	P	MS	F	P
Tidal range										
Estuary type	5	21·19	7·629	<0·001	23	5·447	0·001	17·16	5·585	<0·001
Tide	1	18·09	6·512	0·014	0·014	0·003	0·954	0	0	0·99
Error	46	2·778			4·224			3·072		
Total annual runoff										
Estuary type	5	13·55	4·342	0·003	34·05	8·541	<0·001	15·06	5·032	0·001
Total annual runoff	1	2·322	0·744	0·393	10·95	2·747	0·104	3·646	1·218	0·275
Error	46	3·121			3·986			2·992		
Salinity										
Estuary type	5	21·34	6·796	<0·001	32·72	7·761	<0·001	19·75	6·46	<0·001
Salinity	1	1·438	0·458	0·502	0·362	0·086	0·771	0·661	0·216	0·644
Error	46	3·14			4·216			3·057		
%silt/clay										
Estuary type	5	17·88	11·03	<0·001	15	3·453	0·014	14·21	8·274	<0·001
Silt/clay	1	7·552	4·66	0·039	3·28	0·755	0·392	12·79	7·451	0·011
Error	30	1·621			4·344			1·717		

Edgar *et al.*, 2000). Species richness provided a poor indication of human disturbance in Tasmanian estuaries, largely because mudflats and sandflats contained faunas of similar species richness, as evident in the low correlation between population density and species number (Table 4). The Abundance/Biomass Comparison method for detecting human impacts (Warwick, 1986) also lacked usefulness because many of the infaunal mudflat species associated with high human population densities possessed relatively large body size and biomass (e.g. *Tellina deltoidalis*). Dauer *et al.* (1993) have described similar problems in using the ABC method to detect stressed estuarine communities.

Furthermore, multivariate methods that incorporate environmental variables into a predictive model based on undisturbed habitats, and then assess the difference between observed and predicted assemblages (e.g. Moss *et al.*, 1987), are also unsuitable for identifying impacted sites if sediment characteristics are included in the model. Such models will always predict a mudflat fauna for site with muddy sediments when sediment characteristics are incorporated as a habitat factor into the model.

Anthropogenic impacts on biota in Tasmanian estuaries

Macrofaunal species living in the upper and middle reaches of Tasmanian estuaries are adapted to a physical environment that undergoes rapid and extreme fluctuations in salinity, temperature, water flow and turbidity. Most estuarine species also appear to be resilient to the effects of human disturbance. None of the major community metrics examined (species richness, faunal density, faunal biomass, faunal productivity) were found to be highly correlated with human population density or percent cleared land in catchments (Table 4).

Nevertheless, variation between estuaries in the disturbance indices DI_n and DI_p revealed clear differences between faunal assemblages in estuaries with different levels of human population density. Increasing population density was associated with increasing silt/clay content of sediments and with a reduction in number of epifaunal compared to infaunal species. These changes occurred consistently at relatively low human population densities, with virtually no overlap in DI or silt/clay content of sediments between estuaries with <1 inhabitants km^{-2} and estuaries with >10 inhabitants km^{-2}.

Tasmania is unusual in a global sense in retaining a large number of estuaries with <1 inhabitants km^{-2}. If similar relationships with population density also apply in other regions, then biological communities in most temperature estuaries worldwide should be considered to have already undergone major shifts as a result of human activity. Comparable studies conducted in most countries would possibly show little anthropogenic effect because of a lack of ‘ pristine ’ reference sites.

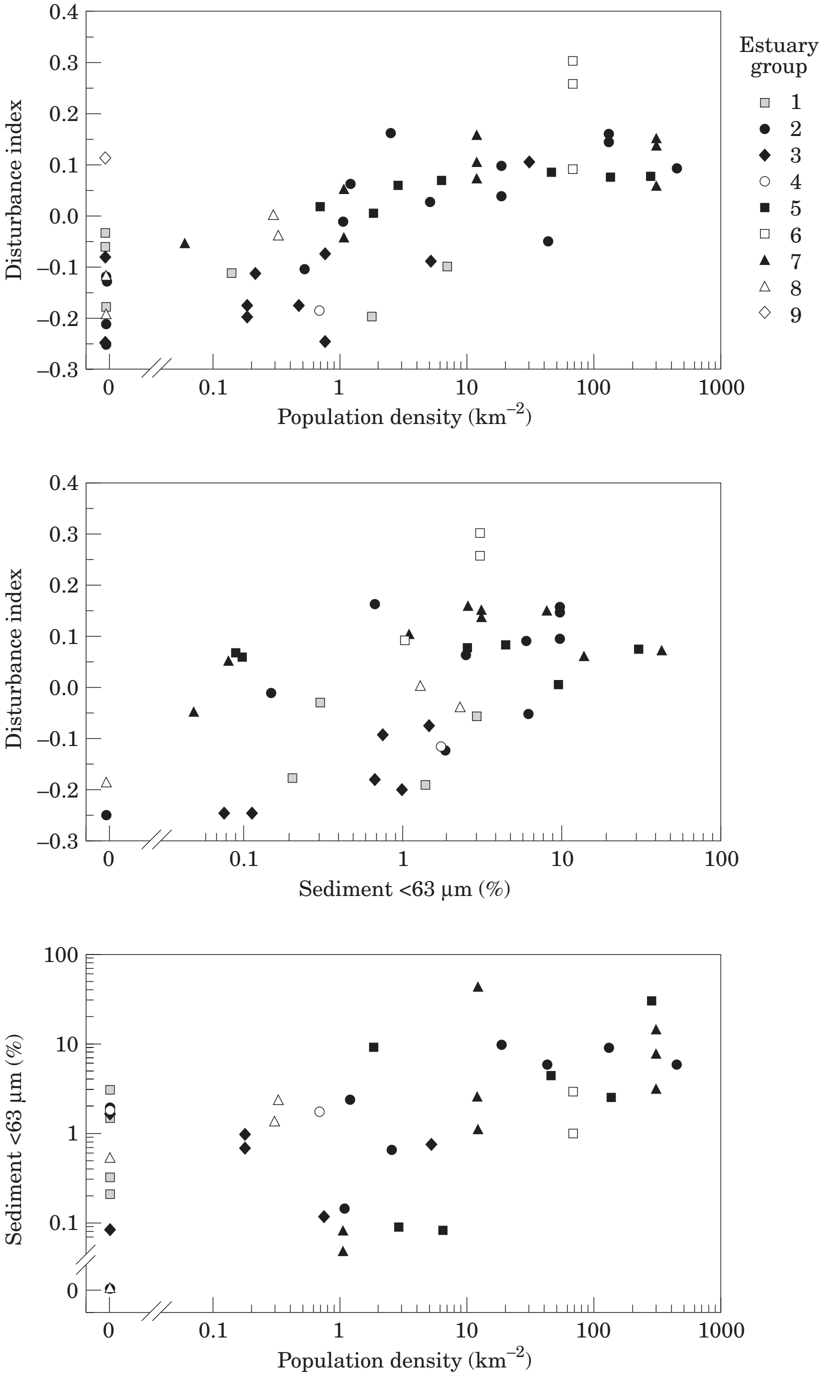


FIGURE 4. Scatterplots showing relationships between the faunal disturbance index DI_n for sites located in estuaries grouped by morphological and hydrological similarities, human population density in catchments, and the silt/clay content of sediments. Note log format of density and silt/clay axes, and discontinuity of origin.

The correlations between human population density, silt/clay fraction of sediments and faunal composition may be due to direct dependence between these factors, or to indirect associations arising from shared relationships with other factors. Given the large number of studies that identify direct causal relationships between human activities in catchments and increased sediment loads (e.g. Campbell & Doeg, 1989), the most likely hypothesis relating these factors is that anthropogenic activity in catchments and around estuary margins causes large inputs of fine suspended sediments that are transported to and

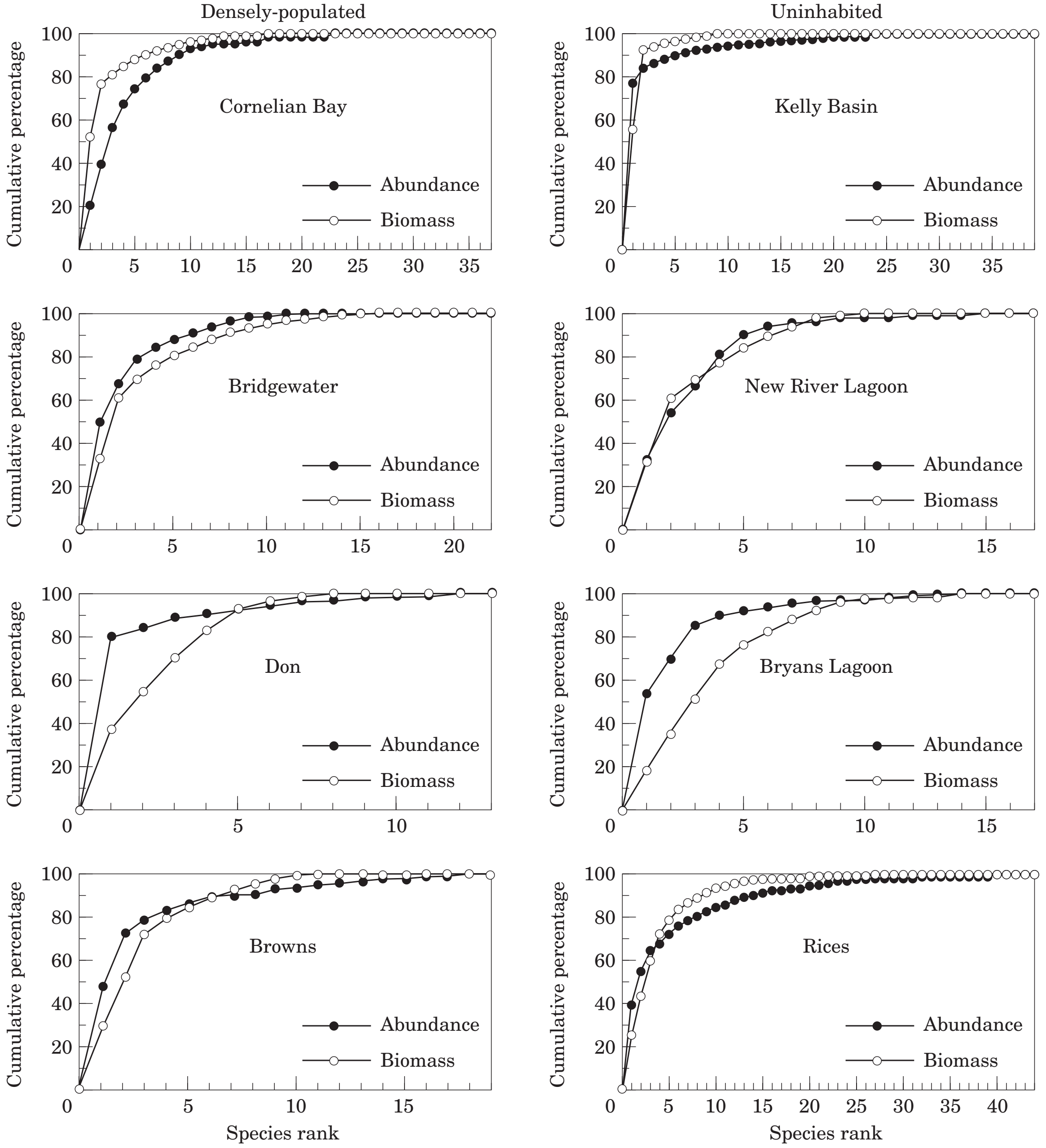


FIGURE 5. Abundance/biomass comparison plots for four sites in estuaries with highest human population densities and four sites in uninhabited estuaries.

deposited in the lower reaches of estuaries. These fine deposits coat the estuarine bed and eventually convert sandflats into mudflats, which attract infaunal species (such as *Tellina deltoidalis* and *Magelona* sp.) and displace epifauna (such as *Eubittium lawleyanum* and *Zeacumantus diemenensis*).

An alternative hypothesis is that human settlement, with resulting high population densities, preferentially occurs in estuaries with muddy rather than sandy sediments, perhaps because of richer soils for agriculture in the hinterland. While this hypothesis cannot be discounted outright, it is less likely than the previous hypothesis given the interspersion of estuaries with high and low human population densities studied around the state, and the extremely consistent relationships between human population density, silt-clay content of sediments and DI_n.

More importantly, results of the ANCOVAs indicated that DI_n and DI_p both increase with increasing human population density and silt/clay content of sediments within estuaries of similar geomorphological and hydrological type. Anecdotal information also consistently indicates that as human population density increases within catchments the foreshores of associated estuaries change from sandflat to mudflat. For example, Cornelian Bay in the lower Derwent estuary possessed a sandy beach until *c*. 1940, but the shore has since degraded and now includes large quantities of silt and clay (Sustainable Development Advisory Council, 1996).

While siltation is clearly an important factor associated with human impacts within estuaries, other factors also probably contributed to faunal differences between estuaries with low and high human population densities. This is indicated by the substantially lower correlation coefficient between *DI* and silt/clay content compared with *DI* and population density (Table 4), and the poor correspondence between silt/clay content and faunal assemblage type (Figure 1). Amongst the most probable contributing factors associated with human impacts are nutrification, eutrophication, seagrass loss and discharge of urban and industrial waste. Manipulative experimental work is required to distinguish between the influences of these and other potentially-important factors.

Acknowledgements

Amongst the many people who made the project possible, we would particularly like to thank Dave Graddon for undertaking the GIS work. The project was supported by funding from Ocean Rescue 2000 (Environment Australia) and an ARC Research Fellowship.

References

Bamber, R. N. & Spencer, J. F. 1984 The benthos of a coastal power station thermal discharge canal. *Journal of the Marine Biological Association of the United Kingdom* **64,** 603–623.

Boynton, W. R., Hagy, J. D., Murray, L., Stokes, C. & Kemp, C. 1996 A comparative analysis of eutrophication patterns in a temperature coastal lagoon. *Estuaries* **19,** 408–421.

Campbell, I. C. & Doeg, T. J. 1989 Impact of timber harvesting and production on streams: a review. *Australian Journal of Marine and Freshwater Research* **40,** 519–539.

Carlton, J. T. 1989 Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environment. *Conservation Biology* **3,** 265–273.

Carr, M. R. 1996 *PRIMER User Manual. Plymouth Routines in Multivariate Ecological Research*. Plymouth Marine Laboratory, Plymouth, UK.

Clarke, K. R. 1993 Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18,** 117–143.

Cloern, J. E. 1996 Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* **34,** 191–202.

Dauer, D. M., Luckenbach, M. W. & Rodi, A. J. 1993 Abundance biomass comparison (ABC method): effects of an estuarine gradient, anoxic/hypoxic events and contaminated sediments. *Marine Biology* **116,** 507–518.

De Jonge, V. N., Boynton, W. D., D'Elia, C. F., Elmgren, R. & Welsh, R. L. 1994 Responses to developments in eutrophication in four different North Atlantic estuarine systems. In *Changes in Fluxes in Estuaries: Implications from Science to Management* (Dyer, K. R. & Orth, R. J., eds). Olsen & Olsen, Fredensborg, Denmark. pp. 179–196.

DeFur, P. L. & Rader, D. N. 1995 Aquaculture in estuaries: Feast or famine? *Estuaries* **18,** 2–9.

Edgar, G. J. 1990 The use of the size-structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology and Ecology* **137,** 195–214.

Edgar, G. J. 1993 Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. *Oecologia* **95,** 115–121.

Edgar, G. J. & Shaw, C. 1995 The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* **194,** 107–131.

Edgar, G. J., Barrett, N. S. & Last, P. R. 1999 The distribution of macroinvertebrates and fishes in Tasmanian estuaries. *Journal of Biogeography* **26,** 1169–1190.

Edgar, G. J., Barrett, N. S., Graddon, D. J. & Last, P. R. 2000 The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* **92,** 383–397.

Faith, D. P., Minchin, P. R. & Belbin, L. 1987 Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69,** 57–68.

Graddon, D. J. 1997 Characteristics of Tasmanian estuaries and catchments: physical attributes, population, and land use. Master of Environmental Studies thesis, University of Tasmania, Hobart.

Lavery, P. S., Lukatelich, R. J. & McComb, A. J. 1991 Changes in the biomass and species composition of macroalgae in a eutrophic estuary. *Estuarine and Coastal Shelf Science* **33,** 1–22.

McClelland, J. W., Valiela, I. & Michener, R. H. 1997 Nitrogen-stable isotope signatures in estuarine food webs: A record of increasing urbanization in coastal wetlands. *Limnology and Oceanography* **42,** 930–937.

Moss, D., Furse, M. T., Wright, J. F. & Armitrage, P. D. 1987 The prediction of the macro-invertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. *Freshwater Biology* **17,** 41–52.

Newcombe, C. P. & Jensen, J. O. T. 1996 Channel suspended sediment and fisheries: A synthesis for quantitative assessment of risk and impact. *North American Journal of Fisheries Management* **16,** 693–727.

Nixon, S. W. 1995 Coastal marine eutrophication: a definition, social causes, and future consequences. *Ophelia* **41,** 199–219.

Ritz, D. A., Lewis, M. E. & Shen, M. 1989 Response to organic enrichment of infaunal macrobenthic communities under salmonid seacages. *Marine Biology* **103,** 211–214.

Rosenberg, D. M., Bodaly, R. A. & Usher, P. J. 1995 Environmental and social impacts of large scale hydro-electric development: who is listening? *Global Environmental Change* **5,** 127–148.

Saiz-Salinas, J. I., Ruiz, J. M. & Frances-Zubillaga, G. 1996 Heavy metal levels in intertidal sediments and biota from the Bidasoa Estuary. *Marine Pollution Bulletin* **32,** 69–71.

Schlacher, T. A. & Wooldridge, T. H. 1996 Ecological responses to reductions in freshwater supply and quality in South Africa's estuaries: lessons for management and conservation. *Journal of Coastal Conservation* **2,** 115–130.

Silberstein, K., Chiffings, A. W. & McComb, A. J. 1986 The loss of seagrass in Cockburn Sound, Western Australia. III. The effect of epiphytes on the productivity of *Posidonia australis* Hook. f. *Aquatic Botany* **24,** 355–371.

Sustainable Development Advisory Council 1996 *State of the Environment, Tasmania, Volume 1—Conditions and Trends*. Department of Environment & Land Management, Hobart.

Valiela, I., Kremer, J., Lajtha, K., Geist, M., Seely, B., Brawley, J. & Sham, C. H. 1997 Nitrogen loading from coastal watersheds to receiving estuaries: New method and application. *Ecological Applications* **7,** 358–380.

van Dolah, R. F., Calder, D. R. & Knott, D. M. 1984 Effects of dredging and open water disposal on benthic macroinvertebrates in a South Carolina estuary. *Estuaries* **7,** 28–37.

Warwick, R. M. 1986 A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* **92,** 557–562.

Warwick, R. M., Pearson, T. H. & Ruswahyuni 1987 Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. *Marine Biology* **95,** 193–200.

Warwick, R. M. & Clarke, K. R. 1993 Comparing the severity of disturbance: a meta-analysis of marine macrobenthos community data. *Marine Ecology Progress Series* **92,** 221–231.

Whitfield, A. K. 1986 Fish community structure response to major habitat changes within the littoral zone of an estuarine coastal lake. *Environmental Biology of Fishes* **17,** 41–51.

Winemiller, K. O. & Morales, N. E. 1989 Communidades de peces del Parque Nacional Corcovado luego del cese de las actividades mineras. *Brenesia* **31,** 75–91.