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Tidal changes in copepod abundance and maintenance of a summer *Coscinodiscus* bloom in the southern San Juan Channel, San Juan Islands, USA

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ABSTRACT: Tidal currents interacting with complex topographies are common features of coastal environments. These interactions are hypothesized to have significant effects on local plankton distribution and abundance, and therefore on food availability to planktivorous fishes. The purpose of this study was to test the hypothesis that tidal currents interacting with an island archipelago create significant and predictable increases in copepod availability to planktivores. Copepod densities during flood and ebb tides were sampled weekly during July–October of 1995–1997. Copepods of the genera *Pseudocalanus*, *Paracalanus*, and *Corycaeus* were the numerically dominant zooplankton except during a bloom of dinoflagellates (*Noctiluca* spp.) in July 1996. At sampling locations within the main tidal current, median copepod densities were 47 to 252 copepods m^{-3} greater during flood tides. In contrast, median densities outside of the main current were not significantly different between tides. An unexpected finding was the presence of an abundant, large centric diatom (*Coscinodiscus wailesii*), which showed a prolonged bloom from early July through early October in all years. Changes in copepod abundance and maintenance of the *C. wailesii* bloom were most likely caused by the advection of copepod aggregations and nutrients from near or below the pycnocline in the Strait of Juan de Fuca. Conversion of copepod numerical abundance to biomass estimates suggests that tidal differences in copepod abundance could affect fish growth. The predictability of changes in copepod abundance may explain why tidal rips and jets are important feeding areas for planktivorous fishes, as well as for fish predators such as marine mammals and seabirds.

KEY WORDS: Tidal currents · Plankton · Copepods · Diatoms · *Coscinodiscus* · Prey availability · Energy subsidy · Strait of Juan de Fuca · San Juan Islands

INTRODUCTION

Interactions between tides and topographic relief are one class of phenomena that may enhance the availability of nutrients or plankton to marine food webs (Uda & Ishino 1958, Johannes 1981, Wolanski & Hamner 1988, Wolanski et al. 1988, St. John & Pond 1992, St. John et al. 1992). Several authors have argued that interactions between tidal currents and plankton distributions create predictable changes in food availability for planktivores (fishes: Hamner & Hauri 1977, Bray 1981, Kingsford et al. 1991, Noda et al. 1994; seabirds: see review in Hunt et al. 1999; marine mammals: Brown et al. 1979). In particular, there is evidence that changes in copepod density will affect the distribution, feeding success, and growth of planktivorous fishes (Bray 1981, Hobson 1986, Kingsford et al. 1991, Shapiro & Genin 1993, Noda et al. 1994, Anderson & Sabado 1995). However, the few published studies where tidal differences in copepod abundance were measured are of short duration (≤1 wk, except St. John et al. 1992) and do not have sample sizes large enough to test specifically for flood-ebb differences or to evaluate the biological significance of the measured differ-

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ences (n ≤ 7 flood-ebb pairs; Alldredge & Hamner 1980, Gagnon & LaCroix 1982, Leichter et al. 1998). The objectives of this study were (1) to determine whether significant differences between copepod abundance on flood versus ebb tides existed, (2) to investigate the physical mechanisms responsible for any tidal changes in copepod abundance, and (3) to evaluate the potential biological significance of abundance differences to planktivorous fish.

MATERIALS AND METHODS

Study site. The San Juan archipelago in Washington State, USA, and its northward extension, the Gulf Islands of British Columbia, Canada, are known for strong tidal currents; complex horizontal and vertical structure; and large, diverse summertime aggregations of marine consumers, including fishes, marine birds, and marine mammals (Thomson 1981, Lewis & Sharpe 1987). In the San Juan Islands, tidal patterns in the summer distributions of planktivorous juvenile fish (Pacific sandlance *Ammodytes hexapterus* and Pacific herring *Clupea harengus*) and fish predators (seabirds: Alcidae, Laridae; seals: *Phoca vitulina*) suggest that tidal cycles significantly affect local food web dynamics (Lewis & Sharpe 1987, Zamon 2000, 2001). The study area was located in Cattle Pass, at the south entrance to San Juan Channel (Fig. 1). San Juan Channel is the narrowest of 3 channels connecting the Strait of Juan de Fuca in the south to the Strait of Georgia in the north (Thomson 1981). Flooding tidal currents in San Juan Channel flow from south to north; ebbing currents flow north to south.

Hydrographic measurements. Because different water masses are usually correlated with changes in plankton density, I determined the types of water present in and adjacent to San Juan Channel. The San Juan Channel is bounded by 2 bodies of stratified water: the Juan de Fuca Strait to the south and the Strait of Georgia to the north (Thomson 1981). It was possible, therefore, that stratified water could enter the study site from either the south or the north. It was also possible that Griffin Bay, a semi-enclosed bay immediately west of San Juan Channel, may have contained stratified water.

I sampled water profiles at 5 stations along a south-to-north, 12 km transect from the Strait of Juan de Fuca and into the San Juan Channel (Fig. 2; station positions given in Appendix 1). Profiles were taken in late August or early September during spring and neap tides in 1996 and 1997. Therefore I was able to determine local water mass structure at the minimal (neap) and maximal (spring) tidal excursions. Each transect

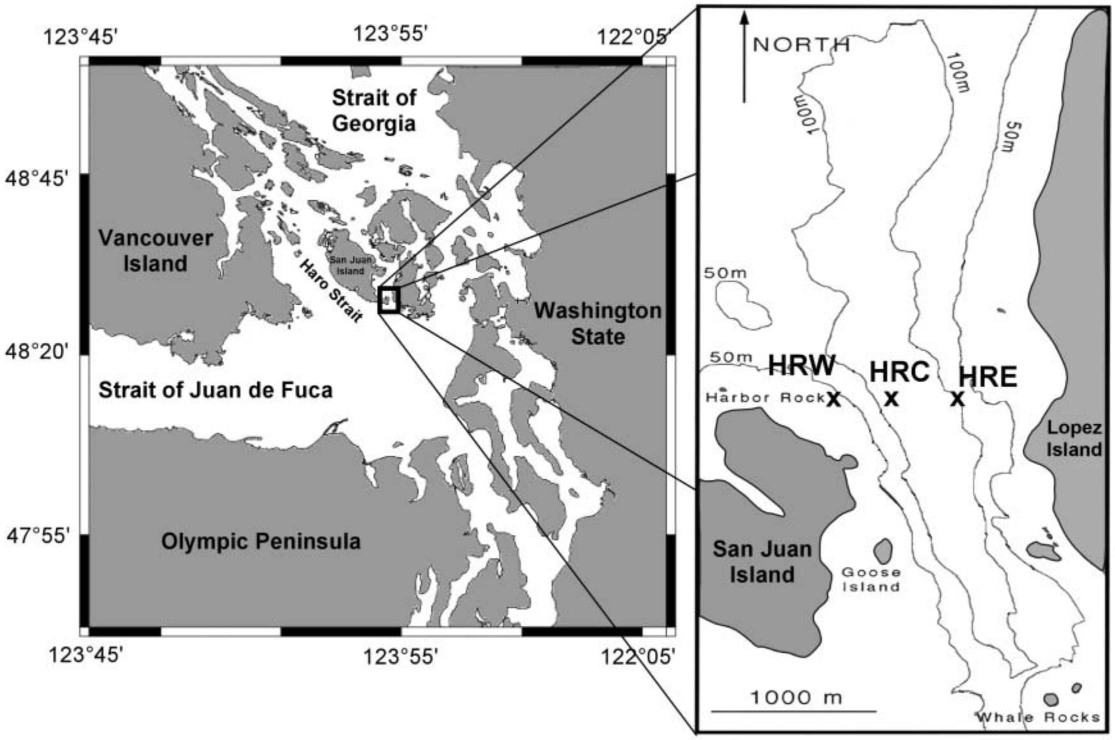


Fig. 1. Study site and net tow stations. Water properties and plankton densities were sampled in Cattle Pass, located in the southern San Juan Channel which runs between the eastern side of San Juan Island and the western side of Lopez Island in the San Juan archipelago. **x**: locations of plankton tows (HRE, HRC, and HRW)

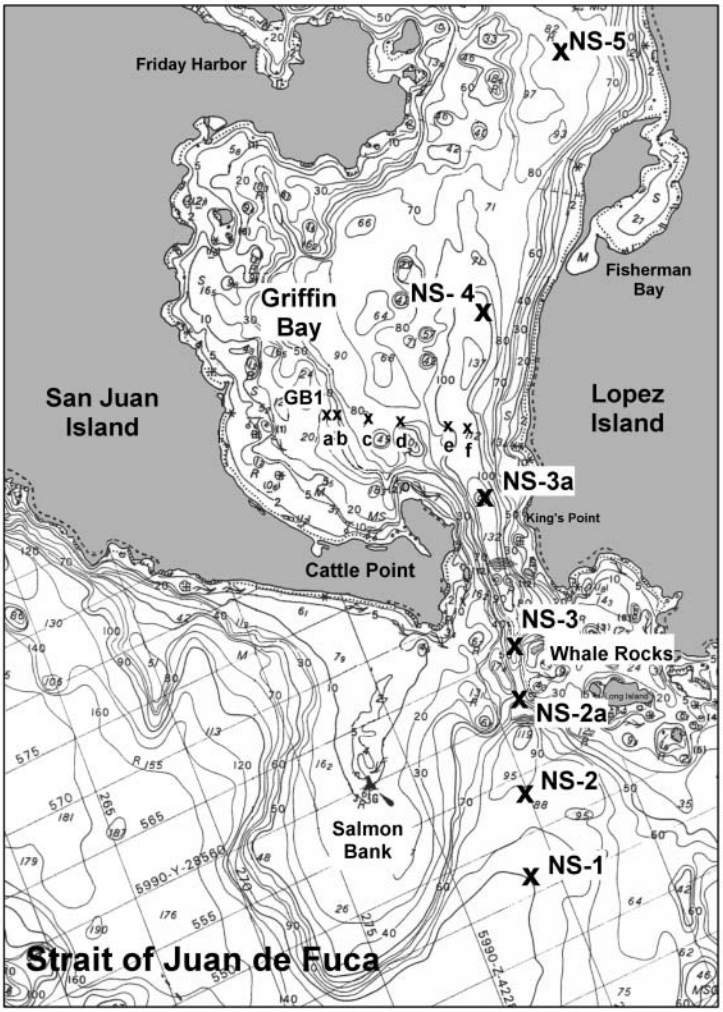


Fig. 2. Locations of temperature-salinity profiles taken during 1996 and 1997. Along-channel stations are indicated by the prefix 'NS', cross-channel stations are indicated by the prefix 'GB-1'. Latitude, longitude, and water depth for each station are given in Appendix 1

took approximately 1.5 h to complete. To determine whether stratified water existed in Griffin Bay, profiles were also taken along a west-to-east, 5.7 km transect from the 30 m contour in Griffin Bay to the eastern side of San Juan Channel (Fig. 2). This transect took approximately 30 min to complete.

I measured temperature and salinity versus depth using a Seabird SEACAT SBE-19 conductivity-temperature-depth instrument (CTD). The CTD was deployed and retrieved by hand with $\frac{1}{4}$" (approx. 6 mm) diameter, 150 m length line marked at 1 m intervals. The instrument was allowed to free-fall to the target depth (downward velocities ~0.75–1.0 m s^{-1}). The CTD casing had 4 acrylic 'fins' strapped to it with hose clamps; the fins kept the instrument falling with a straight trajectory. Profiles were made to 5–10 m above the sea floor or to a maximum depth of 95 m. Temperature and salinity data from the downward cast were averaged in 1 m bins. To visualize changes in water mass properties, I generated contour plots of water properties along a transect with an inverse-distance-squared gridding algorithm (Golden Software 1994).

Net sampling of plankton. Plankton were sampled from a single station in 1995, and then at each of 3 stations along a cross-channel transect in 1996 and 1997 (Fig. 1). Stn HRE ('Harbor Rock East', water depth ~96 m) was located westward of steep drop from 20 to 100 m in the area occupied by a strong tidal jet during flooding currents (surface velocities >1.5 m s^{-1}; Zamon 2000). Stn HRC ('Harbor Rock Central', water depth ~133 m) lay over the deepest part of the channel. Stn HRW ('Harbor Rock West', water depth ~54 m) was located on a relatively shallow shelf west of the main channel; Stn HRW was within a backwater eddy outside of the main north-south tidal flow. Each net tow began at the station's latitude and longitude, but the research vessel (a 4 m Boston Whaler) was allowed to drift with the prevailing current during each net tow.

To compare copepod densities between flooding and ebbing tides, I collected 3 replicate tows from each tide and each station on the same day (3 tows × 3 stations × 2 tides = 18 tows per sampling day). Samples were collected after predicted current velocities in the second half of the tide fell below 1 m s^{-1}, but before slack water. Pairs of flood and ebb tow sets were made once per week during July through October. I chose this sampling scheme because I wanted to sample while currents were still moving, but when water masses and plankton densities were likely to be most different. I chose to sample the top 25 m during daylight hours because the most common planktivorous fish in the area, juvenile sandlance and juvenile herring, feed primarily at the surface during daylight hours (Winslade 1974, Hobson 1986, Field 1988, Batty et al. 1990, Arrhenius & Hansson 1994, O'Reilly 1997).

I sampled plankton with a 0.25 m diameter, 333 µm mesh ring net which had 3.6 kg of iron sash weights suspended below the cod end. The net type was chosen specifically to sample the smaller calanoid copepods (0.5 to 2 mm), which are prey for juvenile sandlance and herring (Field 1988, Haegele 1997). The net was hand-hauled vertically from 25 m to the surface at a rate of 1.5 to 2 m s^{-1} while the vessel drifted at prevailing current speeds during retrievals. No flow meter was used in the opening because the meter would likely have reduced the capture efficiency of the net. Therefore, volume filtered per tow was calculated as

$$\text{volume filtered in m}^3 = \pi\ (0.125\ \text{m})^2\ 25\ \text{m}$$

Of 502 total tows 41 had measurable wire angles greater than zero; these 41 tows were excluded from the analysis to minimize bias due to unknown flow volumes in non-vertical tows.

Plankton were rinsed from the net with pressurized seawater dispensed from a hand-pumped, herbicide-type sprayer. Samples were preserved in 5% buffered formalin and filtered seawater immediately after collection and then sorted in the laboratory with a dissecting microscope. All specimens in each tow were sorted into general taxonomic categories and counted; no subsampling took place, except when densities of large centric diatoms or *Noctiluca* spp. cells exceeded ~2000 m^{-3}. In those cases, diatom or *Noctiluca* spp. cell abundances were subsampled from 200 ml total volume with a 10 ml Stempel pipette. Densities of diatoms and *Noctiluca* spp. from the subsample were extrapolated to the whole volume.

To determine whether any large-scale differences in plankton density occurred with depth, I compared shallow (0 to 25 m) and deep (0 to 80 m) tows. Three slack high and 3 slack low tides were sampled from well-mixed water at Stn HRE in 1997. Two tows were discarded because they became clogged with jellies (total of 34 tows). A strong pycnocline was present at Stn NS-2 during slack high tide, so it was necessary to compare plankton densities above and below the pycnocline in this area. I collected 5 tows from the pycnocline to the surface (shallow tows) and 5 tows from 95 m to the surface (deep tows) during slack high tides.

Statistical analyses. To compare relative numerical abundances of plankton from different taxonomic categories, I calculated the grand total of individuals captured in that taxonomic category in all tows from each station and year. I then divided the number of individuals in each category by the grand total of all plankton captured in that year. This generated relative frequencies for each taxonomic group captured by the net.

For all data, raw densities and natural logarithm-transformed densities were non-normally distributed with heterogeneous variances; therefore parametric tests comparing mean abundances were inappropriate. I used Wilcoxon matched-pair signed-rank tests to compare differences in median plankton densities from flood versus ebb tides at each station on the same sampling day. I selected the paired-sample test because it explicitly compared tides from the same day, thus reducing the confounding effects of daily and seasonal changes on plankton abundance.

I used a Mann-Whitney *U*-test to compare densities between shallow and deep tows. To determine whether or not there was significant between-station variation in plankton abundance, I used matched-pair signed-rank tests to make pair-wise comparisons between stations sampled on the same tide and day.

I used Kolmolgorov-Smirnov tests and Mann-Whitney *U*-tests for independent samples to determine whether there was significant interannual variation in the distribution of plankton densities from the same station. For these tests, data were unpaired and pooled for the same tide; for example, all tows taken in 1995 on the flood tide at Stn HRE were compared with all tows taken in 1996 on the flood tide at Stn HRE. Bonferroni corrections were applied to these multiple comparisons (10 possible comparisons for interannual comparisons, critical p-value = 0.005).

RESULTS

Hydrographic description of southern San Juan Channel

During slack low tides, stratified water was found on 1 of 4 spring tide series at the south of the entrance to San Juan Channel (Fig. 3a: Stns NS-1 and NS-2). The pycnocline appeared at approximately 70 m depth. During slack high spring tides from the same locations, stratified water appeared in all profiles; in all 4 cases, the pycnocline was found at depths between 30 and 40 m (Fig. 3b). Water in the upper layer was generally 10.0–11.5°C and 29.5–31.2 psu, indicating the influence of Fraser River outflow from the Strait of Georgia (Thomson 1981). Water below the pycnocline was generally 7.5–9.2°C and 32.0–33.3 psu; this deeper water resembled deep Juan de Fuca water in its properties (cf. Thomson 1981). Water with temperatures and salinities resembling deeper Juan de Fuca water was also found below 70 m just north of Whale Rocks (Stn NS-3), although a clear pycnocline in the upper water column was absent. Weakly stratified water was found in Griffin Bay (Fig. 4a,b) and north of Whale Rocks inside the San Juan Channel. The relatively unstratified condition in the upper 90 m inside San Juan Channel contrasts with the more stratified summertime conditions known from Haro and Rosario Straits (Thomson 1981).

The very abrupt transition from a strongly stratified condition in the Juan de Fuca Strait to a relatively unstratified condition in the southern San Juan Channel was not an artifact of contouring or sampling distance between stations. It was possible to visualize the strong pycnocline as a continuous, thin line of echo return by recording data from a single-beam, 6° beamwidth, 120 kHz echosounder while travelling on a)

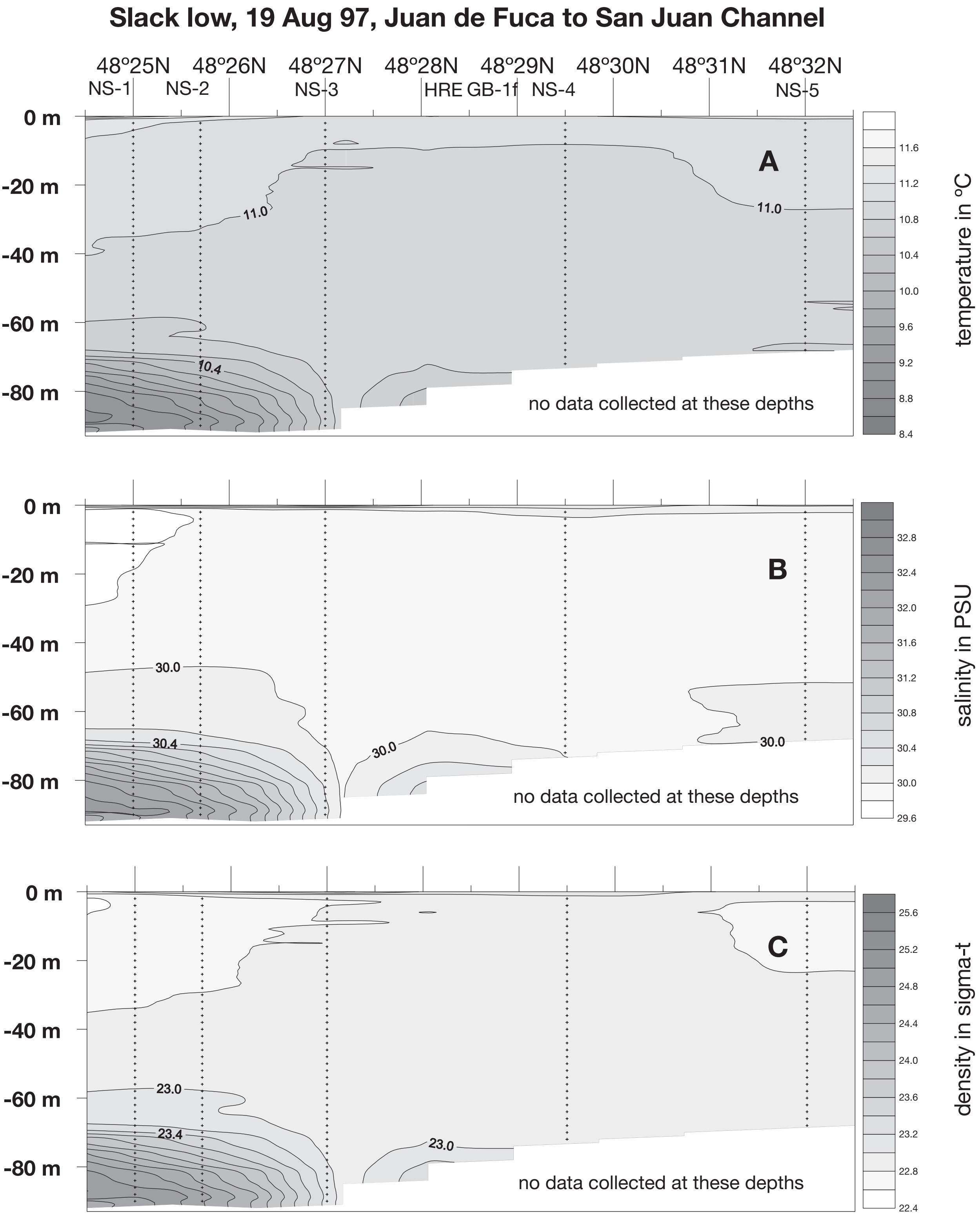
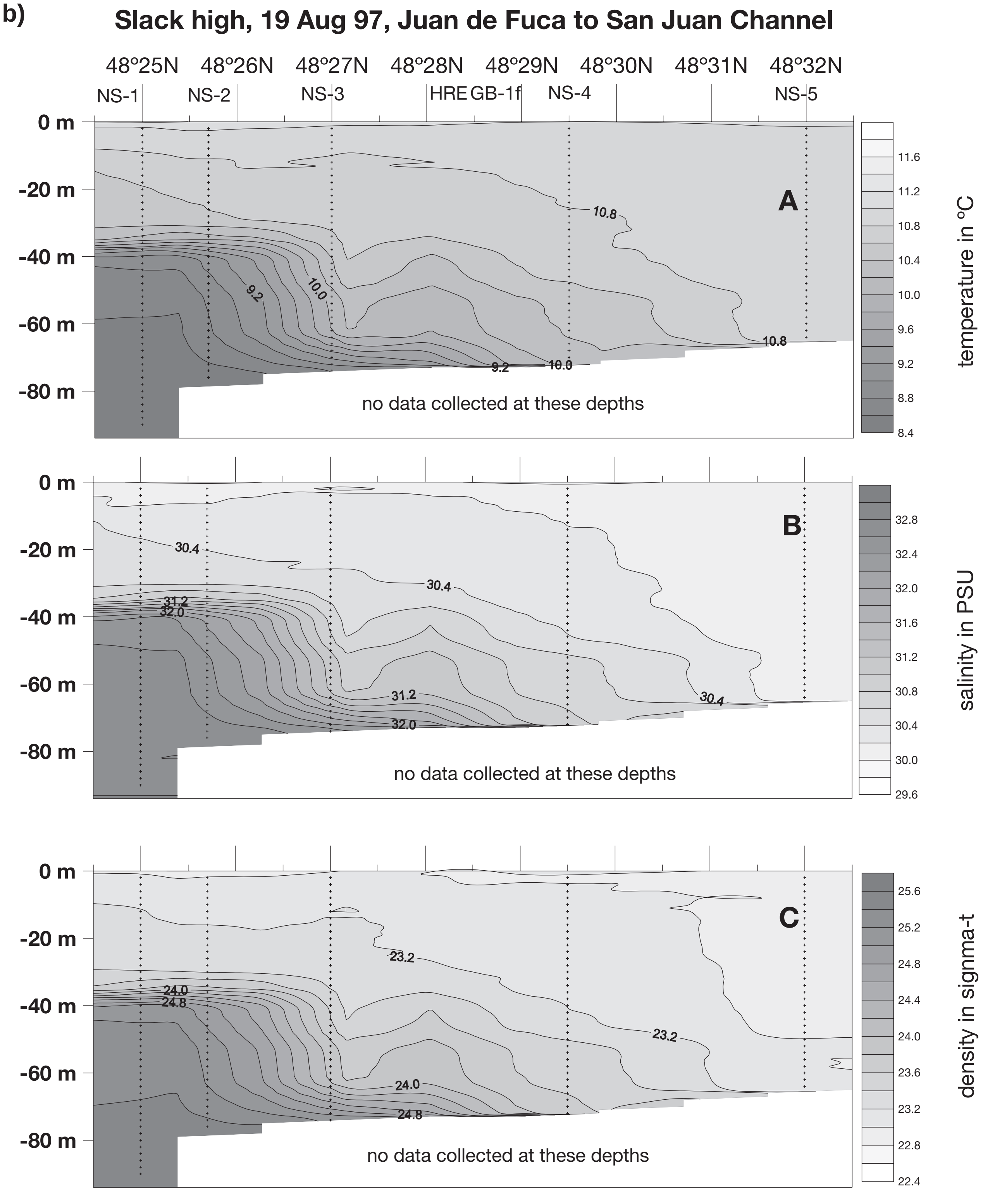


Fig. 3. (Above and following page.) South-to-north profile of Juan de Fuca and southern San Juan Channel, slack (a) low and (b) high spring tides. (A) Temperature, (B) salinity, and (C) density profiles. Vertical lines mark the locations of CTD Stns NS-1 through NS-5; the locations of net tows are indicated above the *x*-axis


b)

Slack high, 19 Aug 97, Juan de Fuca to San Juan Channel

Fig. 3 (continued)

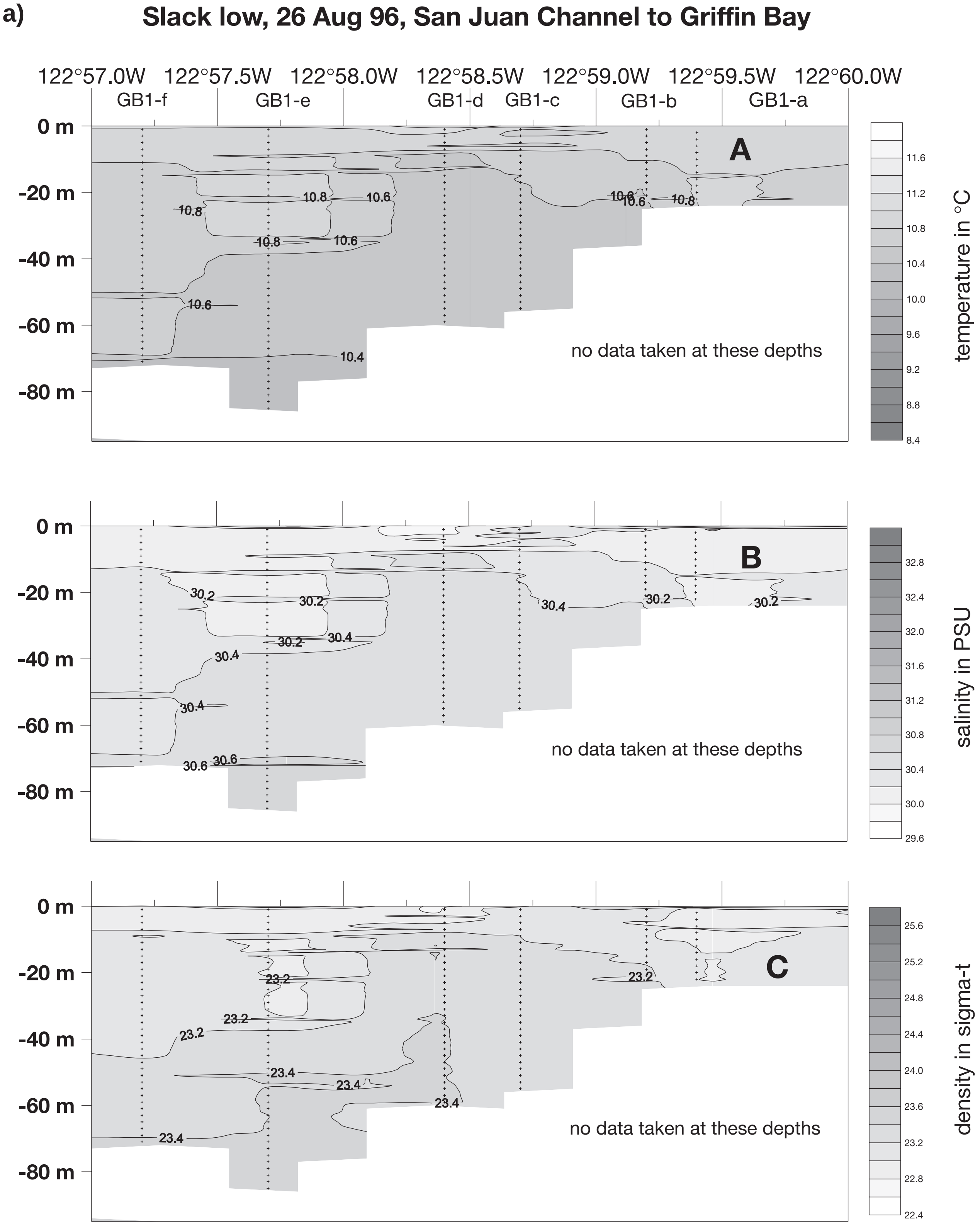


Fig. 4. (Above and following page.) East-to-west profile of Griffin Bay and southern San Juan Channel, slack (a) low and (b) high tides. (A) Temperature, (B) salinity, and (C) density profiles. Vertical lines mark the locations of Stns GB1-a through GB1-f. The inversions near Stns GB1-d and GB1-e are present in the uncontoured data and are not artifacts of the contouring algorithm

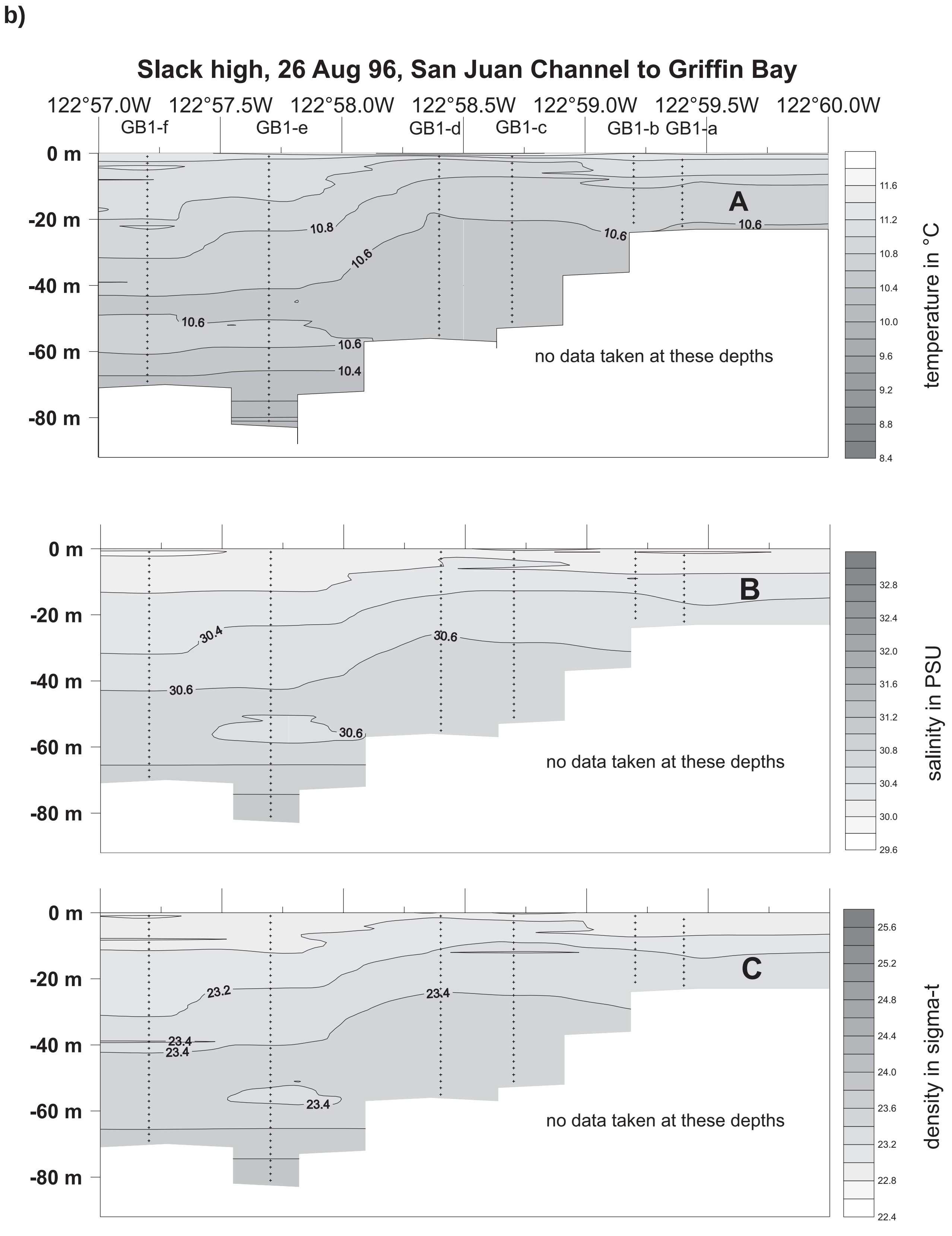


Fig. 4 (continued)

the NS transect line (Fig. 5). CTD deployments confirmed that this thin line coincided with the pycnocline. Acoustic visualizations from tides on 27 August, 31 August, and 2 September 1997 confirmed the 20 to 40 m vertical displacements of the pycnocline between high and low tides just south of Cattle Pass, as well as the fact that a definitive pycnocline was always absent north of the channel constriction near Whale Rocks.

Plankton community composition

Taxonomic categories and their relative frequencies of abundance are listed in Table 1. Large centric diatoms and copepods were clearly the numerical dominants. Only centric diatoms (mostly *Coscinodiscus wailesii*) and small (~1.5 mm) calanoid copepods (mostly *Pseudocalanus*, *Paracalanus*, and *Acartia* spp.) consistently accounted for >5% of all plankton particles captured per year. The only exception to the numerical dominance of diatoms and copepods was a bloom of dinoflagellates (*Noctiluca* spp.) in July 1996. Densities of up to 4700 *Noctiluca* spp. m^{-3} were observed during the bloom. After the first week of August, however, large *Noctiluca* spp. were no longer captured in 1996. *Noctiluca* spp. were extremely rare in 1995 and 1997 samples. The rankings of the top 5 most numerous taxa did not differ among stations in 1996 and 1997, nor did relative frequencies between station pairs ever differ by more than ±5%.

Tidal variation

For the 2 stations located in the main tidal current, median copepod densities showed significant tidal dif-

Table 1. Relative numerical frequencies of plankton taxa

Taxon	HRE 1995	HRE 1996	HRC 1996	HRW 1996	HRE 1997	HRC 1997	HRW 1997
Total plankters	2.1×10^5	1.9×10^5	1.7×10^5	1.6×10^5	5.9×10^4	8.5×10^4	4.6×10^4
Large diatoms							
Centric diatoms	0.884	0.453	0.408	0.416	0.698	0.740	0.689
Other	0.001	0.005	0.001	0.006	0.002	0.001	0.002
Copepods							
Calanoid	0.049	0.271	0.326	0.275	0.125	0.098	0.120
Cyclopoid	0.023	0.026	0.031	0.045	0.046	0.032	0.060
Harpacticoid	<0.001	<0.001	<0.001	0.001	0.001	<0.001	<0.001
Noctiluca spp.	<0.001	0.142	0.108	0.141	0.023	0.021	0.024
Podon spp.	0.004	0.006	0.007	0.007	0.029	0.031	0.034
Gelatinous plankters							
Larvaceans	0.008	0.025	0.028	0.031	0.022	0.014	0.013
Chaetognaths	0.001	0.006	0.006	0.005	0.001	0.001	0.001
Pleurobrachia bachei	<0.001	0.004	0.005	0.006	0.001	0.001	0.001
Siphonophores and cnidarians	0.011	0.020	0.018	0.014	0.008	0.009	0.008
Amphipods							
Hyperiid amphipods	0.001	0.006	0.010	0.008	0.002	0.001	0.002
Gammariid amphipods	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Evadne spp.	0.001	<0.001	0.001	0.001	0.003	0.003	<0.003
Pteropods	<0.001	<0.001	0.001	0.001	<0.001	<0.001	<0.001
Polychaetes	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.004
Ostracods	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Eggs	0.002	0.004	0.004	0.005	0.008	0.005	0.007
Invertebrate larvae							
Barnacle nauplius	0.008	0.020	0.022	0.026	0.016	0.014	0.018
Cyprid	<0.001	0.001	0.001	0.001	<0.001	<0.001	<0.001
Pluteus	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Furcilia	0.001	0.005	0.006	0.007	0.004	0.004	0.007
Zooea	0.001	0.003	0.003	0.003	0.002	0.002	0.004
Megalopae	<0.001	<0.001	0.001	<0.001	0.004	0.004	0.001
Other invertebrates	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Ascidian larvae	<0.001	<0.001	0	<0.001	<0.001	<0.001	<0.001
Fish larvae	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Terrestrial arthropod	<0.001	<0.001	<0.001	<0.001	<0.001	0	<0.001

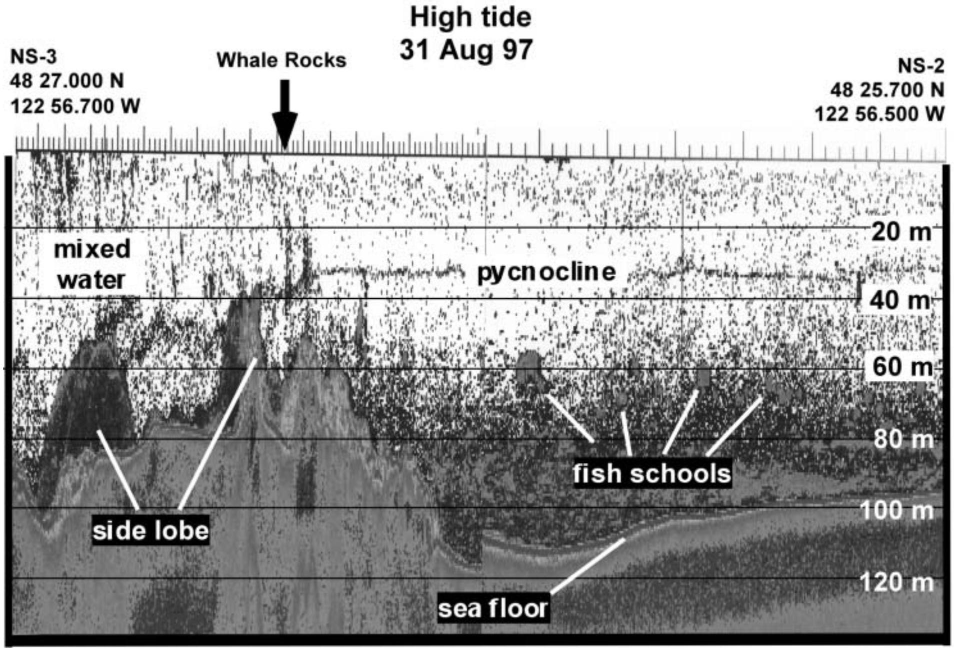


Fig. 5. Water mass structure during high tide at the interface between well-mixed water and stratified water, Whale Rocks, south entrance to San Juan Channel. The location of the pycnocline, visible in this picture as a thin line of echo return at about 37 m, was confirmed with deployment of a CTD. This type of visualization was used to map the vertical and horizontal location of the pycnocline and to target net samples above and below the pycnocline. The minimum channel depth at Whale Rocks is approximately 80 m; echo returns give the false impression of a shallow sill because side lobes return off adjacent channel walls

ferences in 4 of 5 cases: densities were significantly higher on flood tides in all years at Stn HRE and in 1997 at Stn HRC (Fig. 6a–c, Table 2). There was a tendency to have higher densities at Stn HRC for 1996, although the trend was not significant (p = 0.272). For the station located outside of the main tidal current (Stn HRW), densities between tides were not significantly different in either 1996 or 1997.

The presence of a very large centric diatom (*Coscinodiscus wailesii*) was an unexpected and striking feature of the plankton near Cattle Pass in all 3 years (Table 1). Within the main tidal current, *C. wailesii* densities were significantly higher on the incoming tide in 1995 and 1997, but not in 1996. There were no tidal differences at either within-current station during 1996 (Fig. 7a–c, Table 3). Outside of the main tidal current (HRW), there was no significant difference between flood and ebb *C. wailesii* abundance.

Depth variation

In weakly stratified water north of Whale Rocks, copepod densities showed no significant differences

Table 2. Analysis of flood versus ebb differences in copepod densities. Tows with non-zero wire angles were excluded from the analyses. p-values in *italics* are statistically significant

Stn	Year	No. of valid flood-ebb comparisons	p-value of signed-rank test	Median density difference for flood vs. ebb (copepods m^{-3})	Percent of comparisons where median flood density > median ebb density
HRE	1995	16	*0.004*	+62	81
	1996	11	*0.008*	+251	91
	1997	11	*0.028*	+47	73
HRC	1996	12	0.272	+282	67
	1997	11	*0.006*	+76	90
HRW	1996	12	0.695	−40	33
	1997	11	0.248	+11	64

between deep and shallow tows on either slack low or slack high tides at Stn HRE (Fig. 8, Mann-Whitney *U*-test: $p > 0.35$ for both tides). In contrast, copepods in the stratified water at Stn NS-2 were significantly more abundant in deep tows (Table 4, Mann-Whitney *U*-test: $p < 0.01$). For *Coscinodiscus wailesii*, there were no significant differences between deep and shallow densities during slack low tide at Stn HRE (Fig. 8, Mann-Whitney *U*-test: $p = 0.222$), but they were significantly more abundant in deep tows on slack high tides (Mann-Whitney *U*-test: $p = 0.013$). In stratified water, no significant differences were found in comparisons of diatom densities in shallow versus deep tows (Table 4, Mann-Whitney *U*-test: $p > 0.2$).

Between-station and interannual variation

During flood tides, median copepod densities tended to be less for Stn HRW than for either Stn HRC or Stn HRE in 1996 ($p = 0.026$ and 0.06, respectively). No other significant station-station density differences occurred during 1996 or 1997 ($p > 0.10$ in all other comparisons).

Copepod densities were variable but exhibited no obvious seasonal trends within years during the months of July through October. However, Fig. 6 shows that copepods were significantly more abundant at all stations in 1996 than in either 1995 or 1997 (Kolmolgorov-Smirnov tests and Mann-Whitney *U*-tests, all pairwise comparisons significant at $p < 0.001$). Copepod abundances in 1995 and 1997 were not significantly different (Kolmolgorov-Smirnov tests and Mann-Whitney *U*-tests, $p > 0.09$ for flood and ebb). The increased copepod abundance in 1996 appeared to be a community-wide effect: mean densities of *Pseudocalanus*, *Paracalanus*, *Corycaeus anglicus*, and *Acartia* spp. were all approximately 4 times greater in 1996 than in 1997.

For *Coscinodiscus wailesii*, signed-rank tests showed no differences in median densities between Stns HRE and HRC in 1996 or 1997. In contrast, median densities at Stn HRW were significantly less than at both Stns HRC and HRE during flood tides in 1997 ($p < 0.05$). Median densities at Stn HRW were lower than at Stn HRE during ebb tides in 1996 ($p = 0.026$). Otherwise, there were no station-to-station differences in 1996.

During this study, *Coscinodiscus wailesii* abundance increased during early July, and high cell densities persisted through August, September, and early October (Fig. 7a–c). Abundance appeared to decrease during mid- to late October in 1995 and

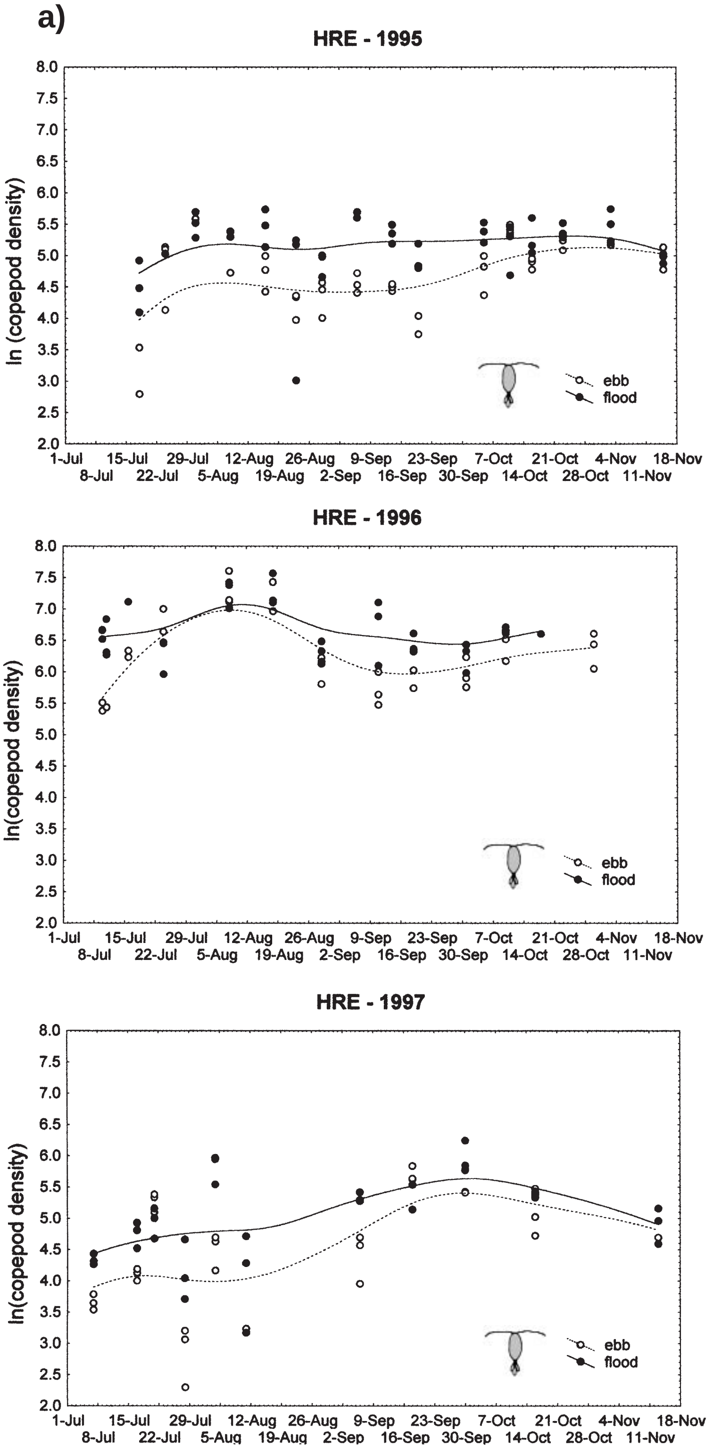


Fig. 6. (Above and following page.) Copepod density versus date. (a) Stn HRE, (b) Stn HRC, and (c) Stn HRW. Raw densities of copepods per cubic meter were transformed to the natural logarithm of raw densities. No tows contained zero copepods. Best-fit lines were drawn using the least-squares method. The lines help visualize seasonal trends and differences in central tendencies between flood and ebb tides, but they have no other statistical significance

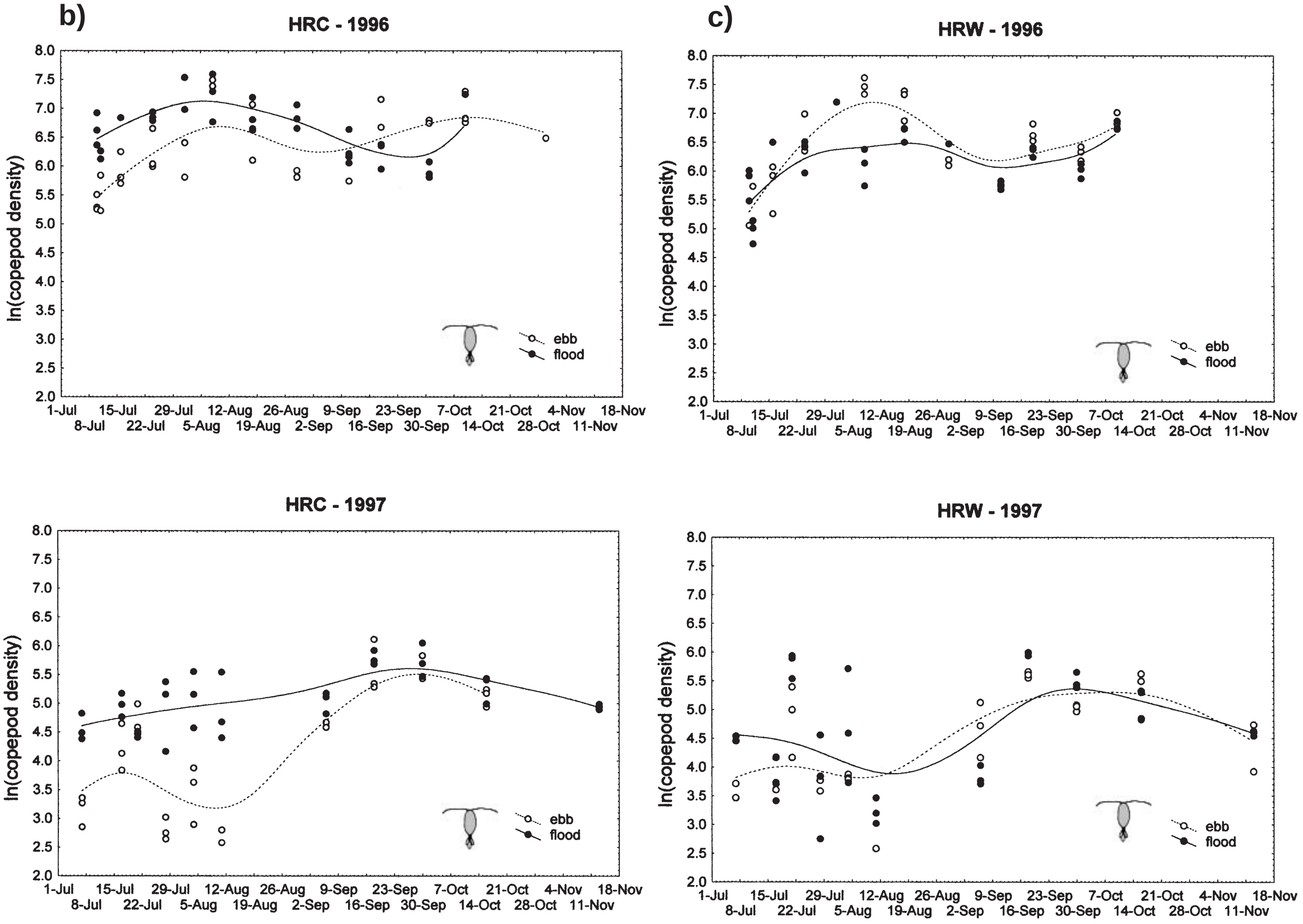


Fig. 6 (continued)

1996 but not in 1997. Changes in abundance within stations between years were significant except for Stns HRE and HRC flood tides between 1996 and 1997 and for Stn HRE ebb tides between 1995 and 1996 (Kolmolgorov-Smirnov and Mann-Whitney *U*-tests, $p < 0.01$ in significantly different comparisons).

DISCUSSION

Tidal changes in copepod abundance: potential causes and effects of advected production

The increases in near-surface copepod abundance within the tidal current but not outside of it support the hypothesis that tidal advection is associated with spatial and temporal changes in food availability to planktivores. Tidal changes in water column properties indicate that colder, saltier water from the Strait of Juan de Fuca is mixed into the San Juan Channel during the flooding tides (Fig. 3b). The source of this water is below the pycnocline in the Juan de Fuca Strait. Copepods were found to be significantly more abundant either near or below the pycnocline. Therefore, it appears that an interaction between animals aggregating near the pycnocline and tidal advection brings copepod aggregations into the surface waters of Cattle Pass from Juan de Fuca. Because estuarine deep circulation in the Juan de Fuca Strait is shoreward at a rate of about 0.1 m s^{-1} (Thomson 1981), any copepods consumed by planktivores could be replenished by advection of animals from the western portions of the Strait.

Within the San Juan Channel, tidal changes in copepod densities appear to be affecting the upper 80 m of the water column as a whole. There were no detectable depth-differences in copepod densities from shallow versus deep tows in the mixed waters of the southern San Juan Channel. Therefore, it is unlikely that changes in surface copepod densities are caused by a redistribution of copepod densities over depth within the San Juan Channel. If this were so, then samples from downwelling, seaward-moving ebb currents should show significantly higher copepod densities in deep tows, whereas samples from upwelling, landward moving flood currents should show significantly higher densities in shallow tows. This was not the case.

Fish distributions and feeding rates, including those of sandlance, have been observed to shift with changes in currents, with fish orienting towards the offshore or upstream side of a topographic feature (e.g. Bray 1981, Johannes 1981, Hobson 1986, Kingsford & MacDiarmid 1988, Shapiro & Genin 1993, Noda et al. 1994, Zamon 2000). Most of these studies have explained this fish behavior as a foraging response to fine-scale changes in plankton supply and abundance. In the 2 studies where plankton densities were measured, locations with higher plankton densities were associated with increases in fish feeding rates, gut fullness, or growth (Bray 1981, Anderson & Sabado 1995). The pattern and magnitude of the density fluctuations observed in the San Juan Channel provide evidence for the fact that tides can change local plankton availability in ways likely to affect foraging success and growth of planktivorous fishes. One can convert the median numerical difference between tides to biomass equivalents with published length-weight equations for copepods. Estimates of the difference in amounts of dry copepod biomass available range between 0.2 and 2.1 mg m^{-3} (Table 5, for median differences of +47 and +282 copepods, respectively). This range of biomass differences is of the same order of magnitude as differences in plankton availability associated with changes in juvenile kelp perch growth (about 0.25 mg m^{-3} from Anderson & Sabado 1995, converting their 1.5 mg m^{-3} wet weight to dry weight, assuming dry weight of copepods is ~16.9% of wet weight, see Omori 1969). Juvenile sandlance and herring were frequently observed feeding in the San Juan Channel, and both species contained copepods as well as *Coscinodiscus wailesii* in their stomachs (O'Reilly 1997, J.E.Z. unpubl. data). There is evidence that the growth of both sandlance and herring can be food-limited (Arrhenius & Hansson 1999, Robards et al. 1999), so tidal rips and channels may be important foraging sites for planktivorous fishes.

Tidal advection may also make copepods available that might otherwise be less accessible to planktivores. Light levels below the pycnocline depth (45 m) in Juan de Fuca are low enough (<1 lux; J.E.Z. unpubl. data) to reduce prey intake in sandlance (Porter 1997). This implies that fish could have higher capture rates when feeding near the surface than when feeding on copepod aggregations near or below the pycnocline within the Juan de Fuca Strait. Turbulence associated with currents may also increase encounter rates or make it more difficult for copepods to detect and escape from an attack.

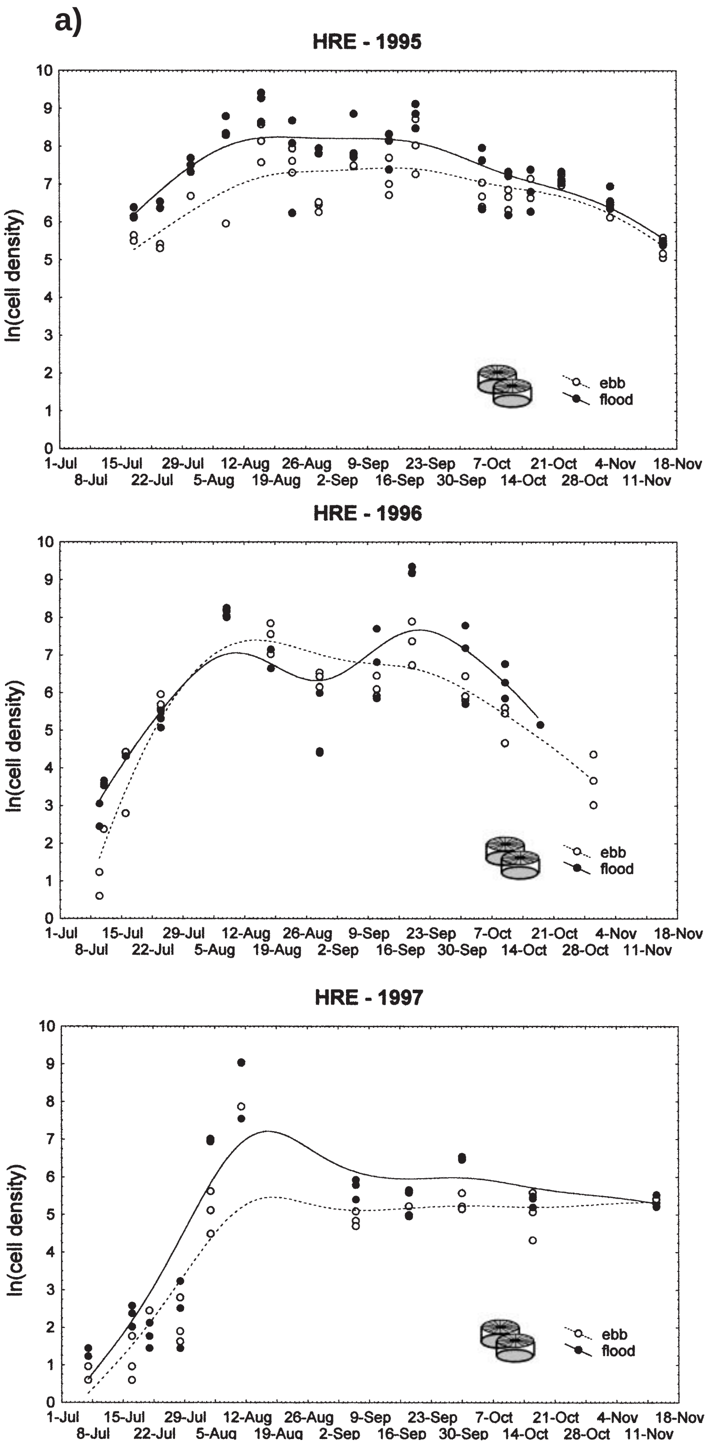


Fig. 7. (Above and following page.) *Coscinodiscus wailesii* density versus date. (a) Stn HRE, (b) Stn HRC, and (c) Stn HRW. Raw densities of cells per cubic meter were transformed to the natural logarithm of raw densities. Seven tows containing zero values were not plotted on these diagrams; all these tows occurred before 6 August. Best-fit lines were drawn using the least-squares method. The lines help visualize seasonal trends and differences in central tendencies between flood and ebb tides, but they have no other statistical significance

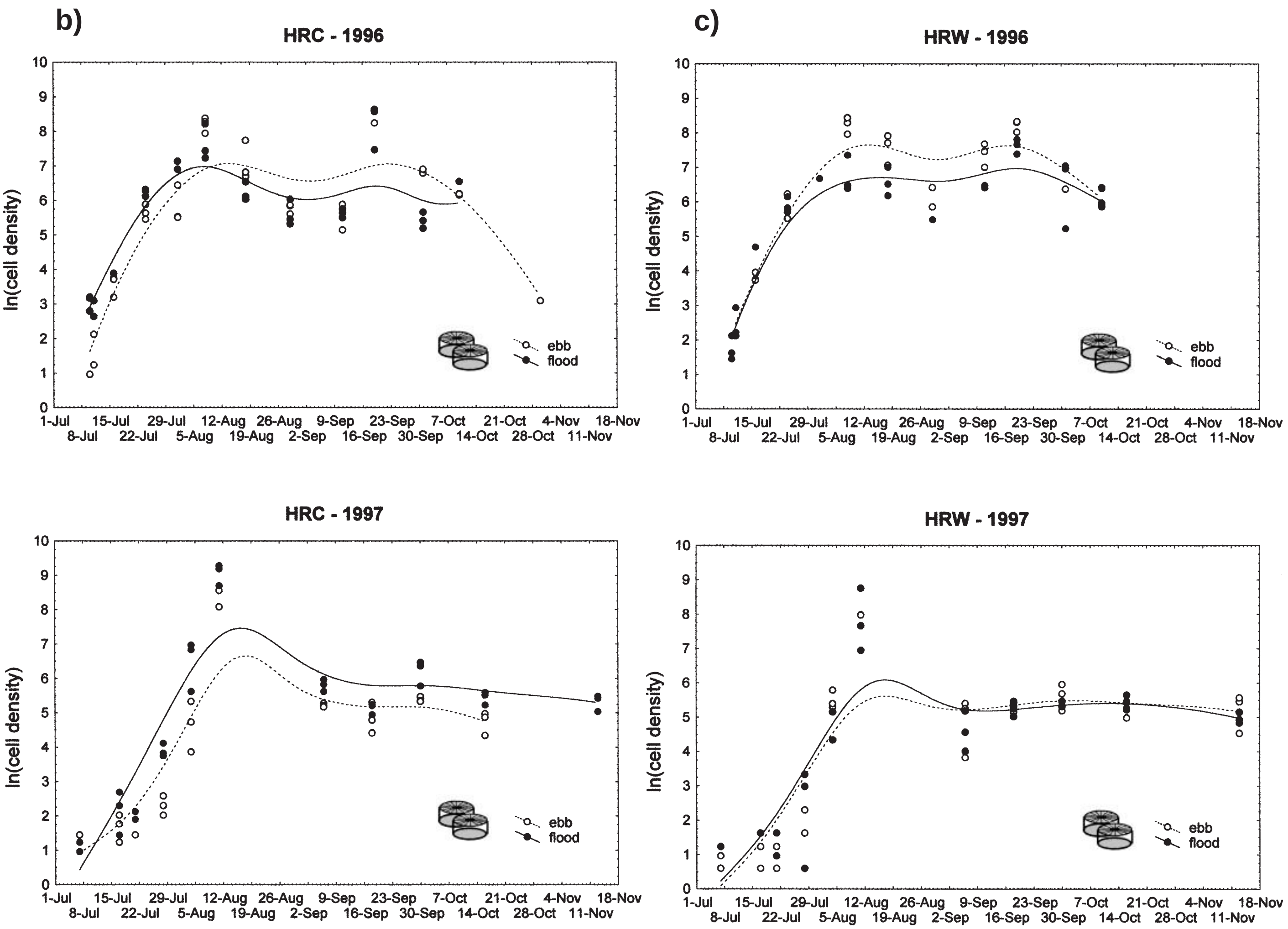


Fig. 7 (continued)

Table 3. Analysis of flood versus ebb differences in *Coscinodiscus wailesii* densities. Tows with non-zero wire angles were excluded from the analyses. p-values in *italics* are statistically significant

Stn	Year	No. of valid flood-ebb comparisons	p-value of signed-rank test	Median density difference flood minus ebb (copepods m^{-3})	Percent of comparisons where median flood density > median ebb density
HRE	1995	16	*<0.001*	+859	100
	1996	11	0.534	+22	64
	1997	11	*0.017*	+70	82
HRC	1996	12	0.638	+10	58
	1997	11	*0.004*	+91	91
HRW	1996	12	0.075	−132	33
	1997	11	0.075	−18	36

Extremely large *Coscinodiscus wailesii*: potential causes and effects of a summer diatom bloom

The numerical dominance of very large *Coscinodiscus wailesii* was an unexpected and striking feature of the biology at this site. The contribution of these large cells to primary production and nutrient dynamics here is unknown, but this diatom was consistently found in the stomachs of Pacific sandlance (O'Reilly 1997, Porter 1997, J.E.Z. unpubl. data) and Pacific herring (J.E.Z. unpubl. data). This is an interesting observation because large cells may, in some cases, provide a sig-

Table 4. Plankton densities per cubic meter in stratified water. Tows were collected from Stn NS-2 at slack high tide, when stratified water was present

Plankton type	Tow type	
	Pycnocline to surface	95 m to surface
Copepods	319.8	591.6
	331.0	657.7
	269.9	645.7
	444.1	578.6
	354.9	624.9
Coscinodiscus wailesii	187.9	168.8
	236.8	191.1
	247.5	182.5
	222.7	262.5
	164.8	195.8

nificant source of nutrition to fish (Horn 1989). Although *C. wailesii* is known to occur in Puget Sound (see Gran & Angst 1931), I found no recently published reports of blooms of this diatom in the Strait of Georgia, Juan de Fuca, or Puget Sound regions. Perhaps this is because most primary productivity studies exclude particles larger than 100 µm (e.g. St. John & Pond 1992). I was unable to find mention of large diatoms in zooplankton studies; this is surprising because *C. wailesii* were such an obvious component of the plankton tows.

Tidal mixing in the Juan de Fuca-Strait of Georgia region is known to increase nutrient concentrations (primarily nitrate) in surface waters (e.g. Parsons et al. 1981, 1983, St. John & Pond 1992, Mackay & Harrison 1997); similar nutrient increases have been reported in other geographic locations (e.g. Wolanski et al. 1988). Local maintenance of higher nutrient concentrations by tidal mixing may explain the extended nature of the *Coscinodiscus wailesii* blooms and the large cell sizes observed in Cattle Pass. The bloom continued well past the April spring bloom that occurs in the stratified waters of the Strait of Georgia (cf. Yin et al. 1997). Although nutrient concentrations were not measured in this study, the tidal fluctuations in temperature and salinity profiles show that deep water is mixed into the San Juan Channel and therefore is likely to maintain relatively high nitrate concentrations throughout the summer. The abilities of *C. wailesii* to survive as resting cells in the dark (Nagai et al. 1995a) and to attain large size through vegetative growth (Nagai et al. 1995b) may be adaptations for living in areas of great turbulence, where nutrient concentrations are high but cells may be mixed into low-light environments for long periods of time.

Blooms of large *Coscinodiscus wailesii* have been reported in the Seto Inland Sea of Japan (Manabe & Ishio 1991) and the German Bight (Rick & Dürselen 1995), where this species can account for up to 90% of phytoplankton biomass retained on 0.2 µm filters. Given cell sizes observed in Cattle Pass (~190 µm radius × 220 µm height), I used Strathmann's (1969) equations to estimate that 1 cell contains about 1.5 µg of carbon; equivalently, 6.6×10^2 cells contribute approximately 1 mg of carbon. Densities of $>10^3$ cells m^{-3} were not uncommon in this study. At the densities observed in Cattle Pass, water columns 1 m × 1 m × 100 m deep would contain almost 1 g of carbon in *C. wailesii* biomass. Because of this diatom's potential importance to the carbon budget and food web, the distribution, seasonal cycle, and population dynamics of *C. wailesii* deserve further investigation.

Table 5. Estimates of median tidal differences in copepod biomass. Prosome lengths of 25 copepods of each taxonomic category were measured with an ocular micrometer. Individuals were from preserved samples collected on 8 August 1996 and 11 August 1997 at Stn HRE. Data are reported as means ± SE. Relative numerical abundances of different copepod types were calculated using all flood tides at Stn HRE. The numerical contribution to median differences was estimated by multiplying median differences from Table 2 by the relative abundance for each copepod category. Biomass was estimated using mean prosome lengths in length-dry weight equations as follows: *Pseudocalanus*, $W = 11.9L^{3.64}$ (Corkett & McLaren 1978); *Paracalanus*, $W = 10^{-8.451}L^{3.128}$ (Liang & Uye 1996); *Corycaeus anglicus*, $W = 10^{-7.17}L^{2.8}$ (Chisholm & Roff 1990); *Acartia* spp., $W = 12.37L^{3.628}$ (Durbin & Durbin 1978); other calanoids, $W = 2.0L^{3.92}$ (Peterson 1979). In these equations, W = dry weight in µg and L = prosome (cephalothorax) length in mm, except for *Paracalanus* and *Corycaeus*, for which L = prosome length in µm

	Year	*Pseudocalanus*	*Paracalanus*	*Corycaeus anglicus*	*Acartia* spp.	Other calanoid
Mean prosome length (mm)	1996	0.92	0.70	0.87	0.84	1.76
	1997	0.92	0.76	0.56	0.88	1.10
Relative abundance (%)	1996	55.2	25.3	7.2	4.3	7.9
	1997	23.9	36.1	21.9	10	7.7
Dry biomass contribution (mg m^{-3})	1996	1.37	0.20	0.07	0.08	0.04
	1997	0.10	0.06	0.01	0.40	0.01

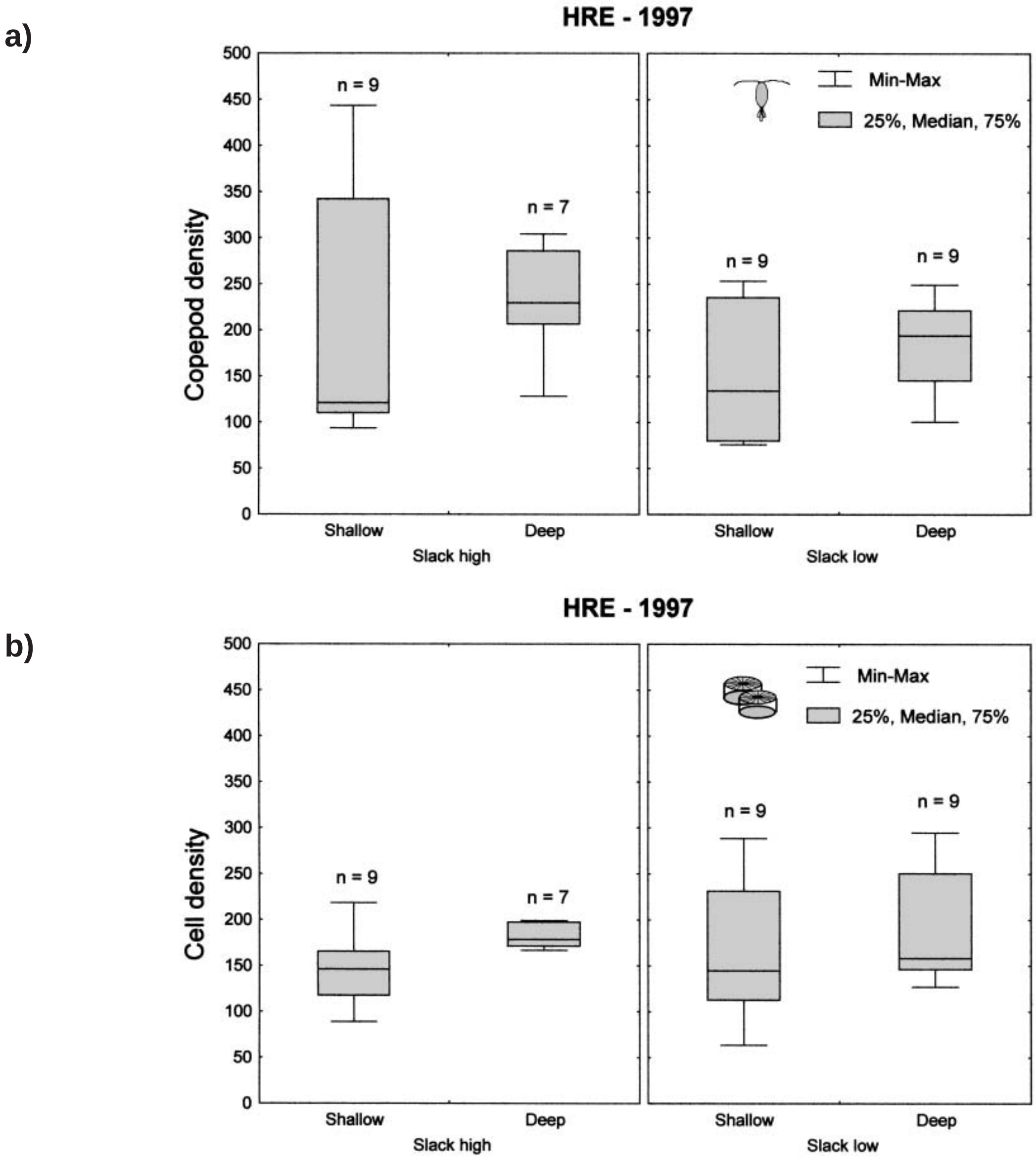


Fig. 8. Deep versus shallow plankton densities in mixed water. (a) Copepods and (b) *Coscinodiscus wailesii*. Shallow tows were collected from 25 m to the surface, deep tows were collected from 80 m to the surface

The general importance of tidally advected production

Advected nutrients and secondary production have been recognized as important factors which may influence food web dynamics in island archipelagos (Uda & Ishino 1958, Johannes & Gerber 1974, Noda et al. 1992, Polis et al. 1997). Tidal currents linking sources of nutrients and plankton to surface waters may act as 'pumps' that rapidly transfer energy to higher trophic levels via planktivorous fishes (this study) or other planktivores (cf. Hunt et al. 1998, Leichter et al. 1998). Tide-topography interactions alter planktivorous fish distribution and behavior in space and time (Bray 1981, Hobson 1986, Shapiro & Genin 1993, Noda et al. 1994, Zamon 2000), which would explain why predators feeding on planktivorous fish also exhibit strong tidal patterns in their foraging behavior (e.g., Braune & Gaskin 1982, Safina & Burger 1988, Zamon 2000, 2001). Tidal currents provide a mechanism to supply what oceanographers call 'auxiliary energy' (Mann & Lazier 1996) and terrestrial ecologists call 'allochthonous energy' (Polis et al. 1997) to local food webs. The predictability of such energy subsidies among years (this study) may help explain the exceptional species diversity and abundance of complex topographic environments in general, and of the San Juan and Gulf Island region in particular.

Appendix 1. Station locations for hydrographic profiles and net tows

Stn	Latitude (N)	Longitude (W)	Water depth (m)	Description
NS-1	48° 25.000′	122° 56.500′	95	Juan de Fuca
NS-2	48° 25.700′	122° 57.000′	105	Juan de Fuca
NS-3	48° 27.000′	122° 57.000′	94	Cattle Pass, north of Whale Rocks
NS-4	48° 29.500′	122° 57.300′	90	San Juan Channel, Rock Point
NS-5	48° 32.000′	122° 56.000′	100	San Juan Channel, Fisherman Bay
GB1-a	48° 28.700′	122° 59.400′	30	Western Griffin Bay, shelf
GB1-b	48° 28.700′	122° 59.200′	40	Western Griffin Bay, shelf
GB1-c	48° 28.700′	122° 58.700′	80	Central Griffin Bay, central basin
GB1-d	48° 28.700′	122° 58.400′	80	Eastern Griffin Bay, central basin
GB1-e	48° 28.700′	122° 57.700′	120	San Juan Channel, west side
GB1-f	48° 28.700′	122° 57.200′	100	San Juan Channel, east side
HRW	48° 28.280′	122° 57.950′	54	Near Harbor Rock
HRC	48° 28.300′	122° 57.600′	137	San Juan Channel, west side
HRE	48° 32.000′	122° 56.000′	96	San Juan Channel, east side

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