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Habitat characters of *Tigriopus californicus* (Copepoda: Harpacticoida), with notes on the dispersal of supralittoral fauna

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Supralittoral splashpools representing 312,000 m^2 of shoreline in Barkley Sound, British Columbia, were surveyed seasonally for tidal elevation, size, water properties, macroflora and faunal constituents coincident with colonization by *Tigriopus californicus* (Arthropoda: Copepoda). Overall, 90.1% of pools containing *T. californicus* were found between 3.0 and 5.0 m above lowest normal tide, with an average surface area-to-volume ratio of 7.06. Copepod populations were found at water temperatures of 6–33°C; salinity of <1–139 psu; pH of 6.1–9.5; and of 1.1–13.7 $mg\,l^{-1}$ oxygen. Sediment and vegetation was sparse in *T. californicus* pools (mean cover 15.79±10.6% in 9.4±11.1% of pools, all species), and consisted most commonly of *Enteromorpha compressa* and *Scytosiphon lomentaria* and its *Ralfsia*-like alternate phase. Common fauna included mites, amphipods, littorines, and nematodes, with the highest diversity of co-inhabitants occurring in spring. Factors such as wind, wave action, and incidental fauna are discussed as potential agents of dispersal for splashpool copepods.

INTRODUCTION

Since the earliest descriptions of the genus *Tigriopus*, its congeners have become familiar subjects in a variety of mensurative and manipulative studies of harpacticoid copepod biology (e.g. Fraser, 1936a,b; Provasoli et al., 1959; Lear & Oppenheimer, 1962; Huizinga, 1971; Harris, 1973; Battaglia et al., 1978; Dethier, 1980; Burton & Feldman, 1981; Kahan et al., 1988). *Tigriopus* copepods are found on the supralittoral fringe of nearly every ocean, including the shores of Japan (*Tigriopus japonicus*), northern Europe (*T. brevicornis*), the Adriatic (*T. fulvus*), North America (*T. californicus*), and New Zealand (the congeners *T. angulatus* and *T. raki*).

Despite their innate physical tolerance and ease of culture in laboratory study, substantive field studies of *Tigriopus* species are few in number (Table 1). These accounts routinely omit critical details of the habitat in which the organism lives, while laboratory studies focus more upon culture methods than specimen collection and natural habitat (but see Lear & Oppenheimer, 1962, p. lxiii).

Splashpools may freeze in winter, evaporate in summer, flood from precipitation and runoff, and accumulate allochthonous shore debris. As a short-lived organism (egg to C–VI adult stage in approximately 21 d at 20°C) (Powlik et al., 1997a), one might assume *T. californicus* to be particularly susceptible to these fluctuations in its environment. Yet *T. californicus* is often described as a generalist feeder (Vittor, 1971; Dethier, 1980), tolerant to a wide range of salinities (normal activity observed at <1–80 psu) and temperatures (in excess of 30°C, including sudden changes of 10°C or more, per Huizinga, 1971; Kontogiannis, 1973). Hence, as an organism that could live ostensibly anywhere in the intertidal zone, it is particularly illustrative to ask why *T. californicus* and its congeners do not.

The exposed water deposits containing *T. californicus* are generally barren, small in size, and may be isolated from the sea for several days without being replenished nor evaporating completely. This not only facilitates access to field sites, but provides natural vessels in which to study changes in chemical and physical properties (Morris & Taylor, 1983) as well as short-term population response (Vittor, 1971; Dethier, 1980; Dybdahl, 1994). The trade-off to this ease of access is the ephemeral nature of small volume pools, which often confounds attempts at long-term monitoring, poses difficulty in the proper use of sampling devices, and magnifies the potential impact of perturbations such pollutants, precipitation, or wave activity, which would be comparatively innocuous in larger enclosures.

The current study proposes to describe the habitat of *T. californicus* in Barkley Sound, British Columbia. Such a description is essential not only to appreciate the general conditions experienced by splashpool organisms, but lends credence to specific conclusions derived from either field or laboratory study. It will additionally provide a partial synthesis of the literature and discuss several ambient agents for dispersal that may act to redistribute *T. californicus* individuals between isolated pools or inhabited outcrops. Actively or passively, what means of dispersal or recovery does the copepod potentially utilize to maintain its position and so ubiquitously yet particularly colonize temperate rocky shores?

MATERIALS AND METHODS

A total of 394 splashpools over 10.4 km of shoreline or 312,000 m^2 were sampled from coastal sites in Barkley Sound, British Columbia, Canada (field sites centred at 50°N 125°10′W). From this initial census, 85 pools were selected using stratified random sampling and monitored

Table 1. *Representative studies of* Tigriopus *field populations and their location.*

Tigriopus californicus Study	Location	Other *Tigriopus* spp. Study	Location
Baker, 1912	Laguna Beach, California	*T. Fulvus* Bozic, 1960	Europe
Monk, 1941	California	Carli et al., 1984	Spain
Egloff, 1966	Mussel Grove, California	*T. brevicornis* Fraser, 1936a,b (cited as *T. fulvus*)	Port St Mary, UK
Vittor, 1971	Charleston, Oregon	Comita & Comita, 1966	Isle of Cumbrae, Scotland (samples from)
Dethier, 1980	San Juan Island, Washington	Clark, 1968	UK
Burton & Feldman, 1981	Los Angeles, California	Harris, 1973	Plymouth, UK
Brown, 1991	Bodega Bay, California	*T. japonicus* Igarashi, 1959	Japan
Dybdahl, 1994	San Juan Island, Washington	Koga, 1970	Fukuoka, Japan
Powlik & Lewis, 1996	Barkley Sound, Canada	Takano, 1971	Sagami Bay, Japan
Powlik et al., 1997b	Barkley Sound, Canada	*T. angulatus/raki* Bradford, 1967	New Zealand
Powlik (this study; 1998)	Barkley Sound, Canada		

Table 2. *Abiotic conditions of Barkley Sound splashpools. Tabulated values are only for those pools found to contain* Tigriopus californicus *populations.*

	Mean water level (m)	Pool elevation (m)	Volume (l)	Surface area (m^2)	Air temperature (°C)	Water temperature (°C)	Salinity (psu)	pH	Oxygen ($mg\,l^{-1}$)
Autumn*									
mean SE	2.01–1.2	3.9–0.8	7–14	4.02–5.8	5.6–4.5	11.3–1.9	27.1–5.6	n.d.	n.d.
range	(−0.1–3.8)	(2.2–6.7)	(0.5–69)	(0.09–30)	(−1.4–11.5)	(6–15)	(1–36.4)		
n	30	143	143	143	26	143	143		
Winter**									
mean SE	2.09–1.3	3.9–1.0	8.9–17	7.01–12.5	5.5–5.2	9.7–1.3	21.4–9.1	7.3–0.2	6.8–0.9
range	(0–3.9)	(1.5–6.7)	(0.1–55)	(0.06–5.0)	(−4–10)	(7–14)	(3.4–32)	(6.2–8.3)	(3.5–10.1)
n	31	114	114	114	21	114	114	42	42
Spring***									
mean SE	1.96–1.2	3.9–0.9	3.8–13	3.87–17.2	17.2–6.1	21.3–2.9	32.5–15.7	7.6–0.7	8.1–2.3
range	(−0.1–3.9)	(2.2–6.7)	(1–113)	(0.1–225)	(8–21)	(10–25)	(0–85.5)	(6.0–9.5)	(1.1–13.2)
n	61	184	184	184	24	184	184	45	45
Summer***									
mean SE	2.03–1.9	3.6–0.8	5.2–67	3.38–6.7	15.5–7.3	24.8–3.2	40.1–17.2	7.5–0.3	6.2–2.5
range	(0–3.9)	(2.0–6.7)	(0–192)	(0–50)	(10–25)	(17–33)	(1.7–139)	(6.0–9.1)	(1.6–10.7)
n	62	312	312	312	34	312	312	39	39

*, values from 1994 only; **, values from 1995 only; ***, values from both 1994 and 1995; n.d., no data; *n*, sample size.

for the remainder of the study. Sampling intervals 1–2 weeks in duration corresponded approximately to changes in season: autumn (September, October), winter (December, January), spring (April, May), and summer (July, August), in the years 1994 and 1995. Whenever conditions permitted, additional pools found to contain *Tigriopus californicus* (Baker, 1912) were also surveyed for biotic and abiotic features, providing the *n* values listed in Tables 2 & 3.

Each pool was mapped according to the variables listed in Tables 2 & 3. Tidal elevation was determined relative to landmarks for known elevation by using local tide tables (DFO, 1995; Canadian Coast Guard, personal communication), and by repeated measure from the waterline using an inclinometer; pool dimensions and volume were determined using a metre stick and 1 m^2 quadrat; and percentage-cover of macroalgae and zoobenthos using a 10 cm^2 quadrat. Salinity was recorded using a Hanna Model 9033 conductivity meter; temperature using a shielded Fisher thermometer; and pH using a Fisher Alkacid full-range pH kit.

Abundance of *T. californicus* was also determined by dividing the surface area of each pool into a numerically-assigned sextet, and a six-sided die was rolled to allow a randomized sample that was repeated in triplicate. Copepods were then sampled using a 30-ml graduated pipette drawn along the pool bottom at these randomly-assigned positions (see Powlik, 1998). Scouring, pumping, or more involved means of sampling water deposits were avoided, as this may have produced an undesirable level of disturbance. Physico-chemical and biotic conditions within and among pools were compared using a

Table 3. *Biotic conditions of Barkley Sound splashpools containing* Tigriopus californicus *populations.*

	Macroflora (percentage-cover)					Fauna		
	Cladophora spp.	*Enteromorpha* spp.	*Scytosiphon* spp.	Encrusting spp. (var.)	Mixed sediment	Percentage of *Tigriopus* pools containing:		Mean ind m^{-2}
Autumn*						5.68	Amphipods (*Traskorchestia* spp.)	
mean ± SE	18.3 ± 6.9	5 ± 0.0	0.0	16.1 ± 2.82	12 ± 7.1	6.82	Barnacles (*Chthamalus*, *Balanus* spp.)	150
range	(5–40)	(5–5)	n/a	(5–30)	(5–40)	2.27	Crabs (*Hemigrapsis* spp.)	0.5
present in	6 of 88	2 of 88	0 of 88	19 of 88	5 of 88	38.64	Littorines (*Littorina* spp.)	90
(%)	6.82	2.27	0.00	21.60	5.68	2.95	Mites (*Neomolgus* and other spp.)	30
						2.27	Sculpins (*Oligocottus* spp.)	1
						1.14	Misc.—*Anthopleura*, *Pisaster*	1
Winter**								
mean ± SE	30 ± 0.0	16.8 ± 2.2	12.5 ± 7.6	5.5 ± 0.6	0.0	2.13	Littorines (*Littorina* spp.)	65
range	(30–30)	(5–30)	(5–20)	(5–10)	n/a	4.26	Nematodes	300
present in	9 of 47	22 of 47	2 of 47	10 of 47	0 of 47	2.13	Sculpins (*Oligocottus* spp.)	1
(%)	19.15	46.81	4.26	21.28	0.00			
Spring***						5.73	Amphipods (*Traskorchestia* spp.)	6
mean ± SE	36.1 ± 6.4	20.9 ± 3.3	20.2 ± 2.6	26.3 ± 3.9	25 ± 6.8	2.08	Barnacles (*Chthamalus*, *Balanus* spp.)	112
range	(10–80)	(5–90)	(5–70)	(5–70)	(10–80)	0.80	Crabs (*Hemigrapsis* spp.)	0.5
present in	14 of 384	44 of 384	47 of 384	26 of 384	10 of 384	12.50	Littorines (*Littorina* spp.)	128
(%)	3.65	11.46	12.24	6.77	2.60	1.30	Mites (*Neomolgus* and other spp.)	46
						1.56	Nematodes	190
						0.78	Sculpins (*Oligocottus* spp.)	1.5
						0.78	Misc.—*Acmaea*, *Pisaster*, *Mytilus*	1
Summer***						3.40	Amphipods (*Traskorchestia* spp.)	4
mean ± SE	28.8 ± 4.6	19.6 ± 4.9	0.0	5.6 ± 0.6	17 ± 1.6	16.06	Barnacles (*Chthamalus*, *Balanus* spp.)	80
range	(5–80)	(5–80)	n/a	(5–10)	(5–40)	0.20	Crabs (*Hemigrapsis* spp.)	1
present in	32 of 498	23 of 498	0 of 498	8 of 498	55 of 498	6.61	Littorines (*Littorina* spp.)	90
(%)	6.43	4.62	0.00	1.61	11.04	1.03	Nematodes	360
						0.41	Ostracods	15
						0.21	Misc.—*Acmaea*, *Pisaster*, *Mytilus*	1.5

*, values from 1994 only; **, values from 1995 only; ***, values from both 1994 and 1995.

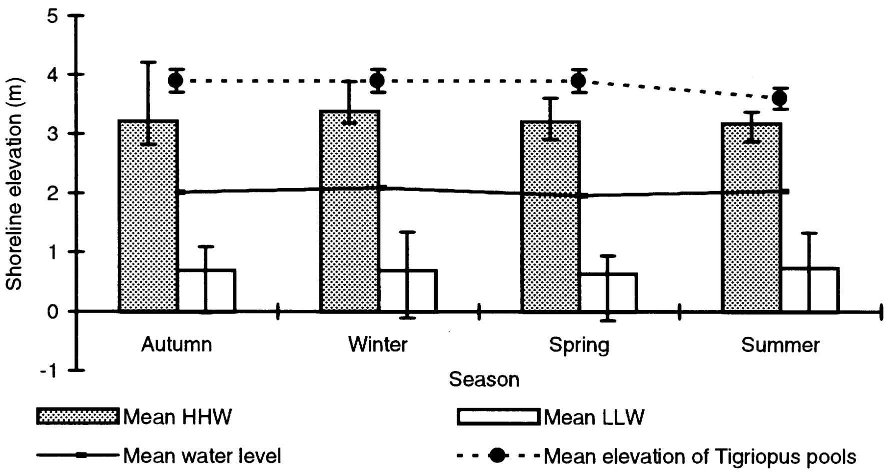

Figure 1. Seasonal elevation of splashpools containing *Tigriopus californicus* relative to mean water level. Water levels are averaged from local tide tables over sampling intervals in each season. HHW, higher high water; LLW, lower low water from mixed, semi-diurnal tide conditions (DFO, 1995). Error bars on dotted line represent 1±SE; lines on HHW and LLW average bars represent maximum and minimum levels during the study interval.

single-factor Kruskal–Wallis analysis of variance by ranks or Mann–Whitney test at $\alpha=0.05$ (Zar, 1984).

RESULTS

The seasonal abundance, abiotic and biotic conditions of *Tigriopus californicus* pools is summarized in Tables 2 & 3. A more detailed analysis of the copepod population structure and its seasonal flux is provided elsewhere (see Powlik, 1998).

Abiotic conditions

From Table 2, the shoreline elevation of pools containing *T. californicus* was remarkably similar over all seasons and field sites, differing only an average of ±0.3 m and remaining above the highest average tide level (Figure 1). Within this restricted range, populations did not necessarily persist throughout the year for those pools that were monitored regularly. Sediment in *T. californicus* pools was most prevalent in the spring, however this feature was also correlated with storm activity and local offshore sources of fine sediment. Both surface area and pool volume were highly variable, however in the absence of vegetation, the relatively large surface of the pools probably assists the diffusion of atmospheric oxygen to dense populations of copepods.

Overall, 90.1% of all *T. californicus* pools were situated between 3.0 and 5.0 m shoreline elevation. Although pool surface area and volume were extremely variable, the ratio of surface area-to-volume was consistently high (7.06 over all sites, seasons). From Table 2, mean pool temperatures consistently exceeded air temperatures and showed less variation, in part from the cooling effects of wind and lithic retention of solar heat. Salinity ranged from nearly freshwater in autumn (diluted by precipitation) to 139 psu in at least one isolated summer pool; the annual mean was 30.2±8.0 psu. While irregularities in pH were not noted in any particular area of the pools, temperature, salinity, and oxygen values were commonly higher at the bottom of pools than nearer the surface.

Biotic conditions

Splashpools containing *T. californicus* are generally devoid of macroflora, with the highest incidences of copepods and visible vegetation occurring in winter (24.11% on average; see Table 3). *Cladophora trichotoma* ('green ball') and *Enteromorpha compressa* ('green confetti') were present throughout the year, and some higher-elevation pools are fringed with *Prasiola meridionalis*, especially those nitrified by guano. Overall algal abundance was lowest in the autumn, with the exception of encrusting species, including *Ralfsia* (common name: 'tar spot') or the *Ralfsia*-like alternate phase of *Scytosiphon lomentaria*.

In winter, only *C. trichotoma* is found regularly, though not in those pools containing *T. californicus* (see Powlik et al., 1997b). *Scytosiphon lomentaria* averages 12.5±4.26%-cover, hence the *Ralfsia*-like alternate phase is rarely observed at this time of year. *Hildenbrandia* spp. are also found in some *T. californicus* pools, however determination of percentage-cover and genera of encrusting algal mosaics, or sporadic tufts of species such as *Endocladia*, was imprecise.

During the highest seasonal abundance, phaeophytic algae and debris may colour pools orange or red; *Hildenbrandia* and *Endocladia* spp. often occur apart from other algae and may become brownish in colour from epiphytic growths of nitzschioid diatoms. In areas of higher wave exposure, *Ulva* may also extend into the lower supralittoral zone, but is not common in *T. californicus* pools.

The presence of *Scytosiphon lomentaria* is entirely suppressed in summer, with the decayed material sometimes leaving a yellowish sediment in *T. californicus* pools. The debris of other macroalgae additionally becomes coated with diatoms and other periphyton (unidentified here, but see Fraser, 1936a; Taylor, 1993). *Enteromorpha compressa* occurrence also diminishes slightly in percentage-cover, but much of this material forms large mats of salt-encrusted filaments superficially devoid of chloroplasts. A second species, *Enteromorpha intestinalis*, occurs more commonly in summer than in spring, when *C. trichotoma* persists as the most common macroalgae.

Table 4. *Incident fauna in Barkley Sound study sites. Species are listed as potential dispersal agents for* Tigriopus californicus.

Incidental or co-occurring macrofauna (Genera)	Classification	Sessile	Motile	Action of transport: Short-distance	Action of transport: Long-distance
Invertebrata					
Anemones (*Anthopleura* spp.)	Anthozoa	X		X	
Amphipods (*Traskorchestia* sp.)	Crustacea		X	X	
Barnacles (*Balanus*, *Chthamalus* spp.)	Crustacea	X		X	
Crabs (*Hemigrapsis nudus*)	Crustacea		X	X	
Littorines (*Littorina* sp.)	Gastropoda		X	X	
Limpets (*Acmaea* sp.)	Gastropoda	X		X	
Starfish (*Pisaster* sp.)	Echinodermata		X	X	
Vertebrata					
Sculpins (*Clinocottus*, *Oligocottus*)	Osteichthyes		X	X	
Marine Mammals (*Eumetopias jubatus*, *Zalophus californianus*, *Enhydra lutris*)	Mammalia		X	X	X
Mink (*Mustela vison*)	Mammalia		X	X*	X**
Deer (*Odocoileus* spp.)	Mammalia		X	X*	X
Black oystercatcher (*Haematopus bachmani*)	Aves		X		X
California gull (*Laurus californicus*)	Aves		X		X
Turnstone (*Arenaria* spp.)	Aves		X		X
Red knot (*Caldris canutus*)	Aves		X		X
Surfbird (*Aphrizia virgata*)	Aves		X		X

*, short-distance transport potential on islands; **, long-distance transport potential on mainland.

Fauna common to *T. californicus* pools or the adjacent shoreline are summarized in Tables 3 & 4. Mites (*Neomolgus*), gammariid amphipods, and littorines (*Littorina* spp.) are most common in the autumn and spring, with barnacles (*Chthamalus* and *Balanus* spp.), limpets (*Acmaea* spp.) and mussels (*Mytilus* spp.) occasionally extending into the lowest *T. californicus* pools. Crabs (*Hemigrapsis nudus*), starfish (*Pisaster* spp.), sculpins (*Oligocottus maculosus* and *Clinocottus globiceps*), and nematodes (unidentified spp.) are also observed in *T. californicus* pools, most commonly in spring, when vegetation is the most plentiful and physical conditions are less extreme.

Avifauna common to Barkley Sound intertidal regions include black oystercatchers (*Haematopus bachmani*), turnstones (*Arenaria* spp.), California gulls (*Larus californicus*), and glaucous-winged gulls (*L. glaucescens*) (J.J.P., personal observation; Campbell et al., 1990). While any of these species might be considered potential dispersal agents for splashpool microcrustaceans, but as an *a priori* consideration, were not collected and examined for the presence of copepods in or on the plumage at the same time as the above data. As season and capture restrictions reduced the number of birds potentially examined at the field site, avian specimens at the Smithsonian Museum of Natural History (Washington, DC, USA) were instead inspected. Examination of all available specimens of bird species known to migrate over the Barkley Sound area, or rocky shores of a comparable latitude, did not reveal the presence of any *Tigriopus* in the plumage or on the appendages. However, other microcrustaceans (unidentified isopoda and copepoda) were found at least once in the plumage of museum specimens identified as *H. bachmani* and *L. californicus*, remarkable if only for the age of the specimens, which ranged overall from 22 to 96 years.

Among the ambient land- and sea mammals, sea lions (*Eumetopias jubatus*, *Zalophus californianus*) and otters (*Enhydra lutris*) are common near at least one of the field sites (Wizard Islet), though at a much lower elevation on the shore and not in the vicinity of the pools surveyed. Mink (*Mustela vison*) and deer (*Odocoileus* spp.) also forage in the high intertidal zone. Leaf, wood, and seaweed debris, insect larvae and allochthonous shore materials are commonly found in the highest *Tigriopus californicus* pools, and may provide the copepods with a source of microflora, dissolved organic matter, or rafting material for short-distance dispersal.

DISCUSSION AND CONCLUSIONS

Abiotic habitat characters

The supralittoral habitat of *Tigriopus californicus* can be likened to an 'intermittent estuary', experiencing as it does the saline influence of wave splash, followed by periods of evaporation or freshwater influx from precipitation and runoff. Steep relief with an accompanying cliff face is a common aspect of shorelines where *T. californicus* pools are found. The bedrock may be granite, limestone, or shale, but a common feature is the protrusion of shelf rocks or benches, forming a raised platform angling sharply into the sea (cf. Lear & Oppenheimer, 1962; Harris, 1973). Flattened foreshores, which flood gradually with the incoming tide and immerse pools by several centimetres appear to be less effective at retaining *T. californicus* populations, perhaps due to the retention of more potential predators or the magnitude of hydrodynamic effects on any microcrustaceans swimming above the bottom. Steep shorelines that produce wave splash may assist the replenishment or redistribution of supralittoral copepod populations on a single outcrop.

While the elevation of *T. californicus* will depend on the degree of shoreline exposure and absolute tidal range, Figure 1 illustrates that in Barkley Sound, *T. californicus* pools remain isolated from average tidal flux, and are probably only inundated by the sea on a few days in each tidal cycle. Dybdahl (1994) made a similar observation, relating this to the ephemeral nature of splashpools, particularly those of a high surface area. Published accounts frequently omit details of water quality and habitat conditions, even though these features directly influence the organisms within the study region (see Morris & Taylor, 1983; Metaxas & Scheibling, 1993). Harris (1973) describes pools of 20-l volume and 30 cm depth during spring sampling of *T. brevicornis*; Dethier (1980, p. 102) observes *T. californicus* pools to be 'usually less than 10-l'. Fraser (1936a) records pool volumes of 7.5–84 l, which compares to the results of Table 2 for some diluted spring pools. However, shoreline topography and high levels of precipitation may drain several small, neighbouring pools into one another, greatly extending the upper limits of this range. The spools surveyed in the current study reflect this, with the greatest pool sizes occurring at the time of highest precipitation in the areas (11.5 mm d^{-1} in autumn and 11.9 mm d^{-1} in winter, from tabulated annual values for the region) although variability in both pool volume and surface area was high and not statistically significant in any season.

The values in Table 2 for temperature, salinity, pH, and oxygen lie within the wide range of published values for these parameters at a comparable latitude (e.g. Harris, 1973; Morris & Taylor, 1983). All *in situ* ranges for temperature and salinity (including Table 2) fall well within the tolerance recorded for *T. californicus* in laboratory culture (Huizinga, 1971; Kontogiannis, 1973).

Biotic habitat characters

In Barkley Sound, the water of splashpools may acquire any number of remarkable colours, including green (from blooms of *Tetraselmis* prasinomonads), orange (from leached phaeophytes or even from the density of resident *Tigriopus* populations), red or yellow (from the tannins in logs or leachates from red or brown algae), white (from bacteria or sulphur production), pink (from *Oxyrrhis* dinophytes) or transparent and colourless (F.J.R. Taylor, personal communication). Decay and putrefaction of algal debris and the bacterial activity promoting this process have previously been related to *Tigriopus* occurrence (Fraser, 1936a). Anthropogenic inputs of nutrients or nitrogen introduction from animal excreta does not appear to enhance *T. californicus* population growth, as has often been assumed anecdotally.

Filamentous *Enteromorpha* and *Scytosiphon* likely utilize the ample supply of freshwater from precipitation and rainfall; the ancillary pigmentation of the phaeophytes may also take advantage of the weaker springtime sunlight. The results of macroflora percentage-cover from Table 3 concur with previously-published values for temperate, supralittoral splashpools.

Among co-occurring fauna, Fraser (1936a) included *Littorina rudis,* ostracods (*Cythere lutea*), *Dactylopusia brevicornis* (Claus), *D. vulgaris* Sars, *Idya furcata* (Baird), *Amphiascus minutus* (Claus), the harpacticoid *Amphiascus minutus*, and *Chironomus* larvae in his field samples of *Tigriopus fulvus*. Dethier (1980) noted littorines, as well as dipteran larvae, grapsid and pagurid crabs in *T. californicus* pools. At the highest shore elevations, Fraser (1936a) found splashpool microcrustaceans to be up to 99.98% monospecific (published as *T. fulvus* but probably *T. brevicornis*, the species endemic to the UK, note Damgaard & Davenport, 1994), in contrast to the highest species diversity, found at the mid-littoral level. From the current observations, *T. californicus* pools are also largely monospecific, with other species rarely exceeding a few individuals per sample. Incidence of these other species (not identified here) also appear to relate to season and the relief of the beach face: spring plankton populations are typically more diverse, and low-relief shores are more likely to contain non-*Tigriopus* specimens.

Dethier (1980) discussed predation as an influence restricting the lower intertidal distribution of *T. californicus*. In her study, *Tigriopus* pools introduced with anemones (*Anthopleura*) or cottids (*Oligocottus*) showed marked reduction in population numbers, and the orange coloration and 'jerky' swimming motion of *Tigriopus* may also make them attractive to visually-oriented predators. Dethier's (1980) work also demonstrated that *T. californicus* can survive in pools lower in the intertidal zone, providing that predators and wave scour are removed.

The number of naturally-occurring aquatic predators in supralittoral pools is scant. Gammaridean amphipods are found in *T. californicus* pools, but have not been observed to feed on *Tigriopus*, nor are they found in sufficient numbers (typically 4–6 ind l^{-1}) to provide significant culling of *T. californicus*. The size of the pool may be too small for most free-swimming predators, and the physical conditions too severe for sessile predators (see Dethier, 1980), hence the most significant agents responsible for culling established *Tigriopus* populations may be only cannibalism, desiccation and wave wash.

Burton & Feldman (1981) suggested that complete extinction of *Tigriopus* populations is unlikely, but regular depletion of populations may occur, either due to wave activity or seasonal changes in climate and water properties. Dybdahl (1994) reported extinction of *T. californicus* populations in 35% of his study pools over a period of six to eight weeks. Occasionally in the present study pools were discovered in which the *T. californicus* were nearly all apparently deceased. Temperature and salinity were not anomalous in these pools (within the limited time of the measurements taken), however this does not preclude the possibility of thermal or haline shock from a rapid change in these parameters or the presence of a localized, unidentified pollutant. These pools may also have been evaporated pools recently hydrated by runoff or wave splash. While wave conditions may be less extreme in the summer, it is suggested that influence of evaporation and stagnation may become much more pronounced, particularly in southern climates. Furthermore, even populations which are trapped in evaporated pools do not necessarily become 'extinct', as there exists the potential for individuals to resume normal activity following rehydration (Powlik & Lewis, 1996).

Agents of dispersal

Regular inshore transport by flood tides should be considered an obvious and significant influence in the distribution of *Tigriopus* populations (Igarashi, 1959; Vittor, 1971), but more so for those pools located at a lower tidal elevation, hence more frequently flushed. Using a vital stain, R. Burnett (personal communication cited in Morris et al., 1980) found pool populations of *T. californicus* to undergo an exchange of nearly half their numbers after a few days, although the net number of individuals changed very little. This suggests not only a potential carrying capacity for pools, probably based on food abundance, but also: (1) *T. californicus* probably do not or cannot relocate to their 'home' pools following wash-out; and (2) 'source' populations of *T. californicus* comprised of displaced individuals may well exist immediately offshore from outcrops or headlands, but these do not disperse or survive in open water long enough to colonize adjacent shores. The disparity between *Tigriopus* populations on neighbouring outcrops and the conspicuous absence of the copepod on sandy beaches or in nearshore water parcels (J.J.P., personal observation; Vittor, 1971) does not support longshore transport as a dominant means of dispersal. This does not suggest the organism is entirely absent in coastal ocean currents, but that its numbers are practically undetectable there—an effect amplified by the difficulties of sampling with nets, pumps, or plankton traps alongside a dynamic, rocky shoreline.

Tigriopus individuals may also achieve short-distance dispersal via rafting on allochthonous materials or natural concretions (Hicks, 1988). However, given the high elevation of most *T. californicus* pools in Barkley Sound (Figure 1), the provision and relocation of raft material would be accompanied by intense wave action, and it would be difficult to determine the contribution of rafts relative to wash action for copepod redistribution.

Microcrustaceans from estuarine areas, salt pools, or lakes may persist in evaporated basins as encysted eggs, to be passively dispersed by wind. From Powlik & Lewis (1996), *Tigriopus californicus* may be similarly rehydrated from virtually all life stages, including the gravid female. Since it is not uncommon for *T. californicus* pools to completely evaporate, exposing the copepods at a density of several thousand individuals per litre. By extension, it is possible that desiccated *T. californicus* waifs are dispersed by wind, and potentially carried to an area providing more immediate moisture replenishment. The numerical abundance in some pools may make them good candidates for incidental collection on the plumage or appendages of foraging birds. The coastal area extending through Barkley Sound from Baja, California, to the Arctic—the described range of *T. californicus*—is a major migratory corridor for dozens of bird species, with some of these (red knot, *Calidrus canutus*) extending their range to western Europe, (the locale of *T. brevicornis* and *T. fulvus*). Assuming a 10–15% recovery of desiccated individuals (Powlik & Lewis, 1996) from a founding population of eight to ten individuals (Vittor, 1971; Dybdahl, 1994), only 100–150 *Tigriopus* retained by a bird (or birds) foraging in the supralittoral zone would be sufficient to act as a means of dispersal.

Egloff (1966) proposed grapsid and pagurid crabs as potential carriers of *T. californicus* between pools in California. From a limited data set ($n=5$ *Pachygrapsus crassipes*), all life history stages and as many as 73 individuals were found on a single *P. crassipes* carapace, though the density of the source *T. californicus* population is not provided. Egloff's (1966) suggestion is commonly reiterated in the literature (as by Dethier, 1980; Burton & Feldman, 1981; Dybdahl, 1994), without any conclusive evidence in support of this mechanism. In the Barkley Sound, *Hemigrapsis nudus* is the only crab found consistently in *T. californicus* pools; no published 'home range' for the species is known, however hitchhiking on larger Crustacea is doubtfully as effective as wave surge for mass redistribution of copepods within metapopulations. The viability of copepod redistribution on crabs or starfish may additionally be lessened by: (1) the carrier moving lower on the shoreline (into pools of higher exposure to waves, or higher abundance of predators); or (2) the increased potential for predation by visually-oriented predators, including birds, by associating with a larger, more conspicuous invertebrate. *Tigriopus californicus* itself also crawls well in the rivulets and moist areas between adjacent pools.

Land mammals including the mink, deer, and domestic pets observed at several study sites may redistribute copepods among supralittoral water deposits, but this does not explain the degree of island colonization observed for *Tigriopus*. Although not classified as parasitic, adult *Tigriopus* are aggressively thigmotactic, and have been observed attaching themselves to the gills of fish. It is doubtful that any fish would survive the physical conditions of a typical *Tigriopus* pool (see Dethier, 1980), and transport in this manner would most likely carry the copepod downslope into less hospitable conditions. An evaluation of sea mammals as incidental carriers of *Tigriopus* individuals has not been performed.

In summary, the supralittoral habitat of *Tigriopus californicus* is highly dynamic and spatially and temporally heterogenous. Ambient macrofauna provided the most obvious demarcation of season and tidal elevation, although colonization by *T. californicus* appears to occur irrespective of the percentage-cover of vegetation. The extreme flux in physical conditions experienced in supralittoral pools may create an ephemeral habitat for *T. californicus*, but one that significantly restricts the presence of potential predators or competitors over much of the year.

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