ECOLOGY OF *TIGRIOPUS CALIFORNICUS* (COPEPODA, HARPACTICOIDA) IN BARKLEY SOUND, BRITISH COLUMBIA

BY

James John Powlik

B.Sc. (hons.), The University of British Columbia (1988)
M.Sc., The University of British Columbia (1990)

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Department of Oceanography
The University of British Columbia
1461 - 6270 University Blvd.
Vancouver, B.C.
CANADA V6T 1Z4

Date: 30 APRIL/96

ABSTRACT

The thesis addresses several aspects of the habitat characters and population attributes of the splashpool copepod, *Tigriopus californicus* (Baker) in Barkley Sound, British Columbia. Overall, 90.1% of pools containing *T. californicus* were found at 3.0 to 5.0 m above lowest normal tide, with an average surface area-to-volume ratio of 7.06. Copepod habitation was found at water temperatures of 6 to 33°C; salinities of less than 1 to 139‰; hydrogen ion concentrations (pH) of 6.1 to 9.5; and oxygen levels of 1.1 to 13.7 $mg \cdot L^{-1}$. Vegetation and sediment were sparse in *T. californicus* pools (15.79 ± 10.6% cover in 9.4 ± 11.1 % of pools, mean ± S.E.); with the most common macroalgae including *Enteromorpha compressa, Scytosiphon lomentaria* and its *Ralfsia*-like alternate phase. Incidental invertebrates and vertebrates that may act as potential agents of dispersal for *T. californicus* and its congeners are also listed and discussed relative to the world-wide biogeography of the genus.

In an analysis of the copepod's association with chlorophytic macroalgae, pools and laboratory microcosms containing the alga *Cladophora trichotoma* retained fewer surviving *T. californicus* (18.6 ± 7.3%) compared to treatments containing *E. compressa* (93.8 ± 5.4%) or without vegetation (95.6 ± 0.1%); the susceptibility of mature *T. californicus* to a possible crustacean deterrent produced by *C. trichotoma* may preclude the establishment of copepod populations. In a second experiment, apparently dead *Tigriopus californicus* were enlivened following re-hydration with either fresh or sea water, with gravid females and adult males demonstrating the greatest response (10.7 ± 8.5% recovery overall).

Development and body length were also compared under conditions representative of *in situ* summer (18 - 20°C; 30 - 32‰ salinity) or winter (10 - 15°C; 20 - 25‰ salinity) conditions. Total generation time (egg to adult) was 21 days under summer conditions, and 30 days under winter conditions, though no net difference in body length was observed. Clutch size was 20 ± 4.2 eggs at 10 - 15°C and 26 ± 8.1 eggs at 18 - 20°C for females in culture; field specimens had a mean clutch size of 23 ± 6.5 eggs in winter (January), increasing to 37 ± 10.2 eggs · clutch^{-1} in summer (July and August). Population density ranged from 217 ± 401.7 individuals · L^{-1} in winter to 835 ± 1750.6 individuals · L^{-1} in summer, exceeding 20,000 individuals · L^{-1} in some pools. A synthesis of these results with previous studies is provided, including suggested parameters for estimating population flux.

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ACKNOWLEDGMENTS

The *Auu ay aht* Indian Band are duly thanked for providing access to the field sites around southeastern Barkley Sound. K. Allcock and M. N. Madryga assisted with the collection of data and Dr. G. R. Graves and L. Rimmer provided access to archived materials.

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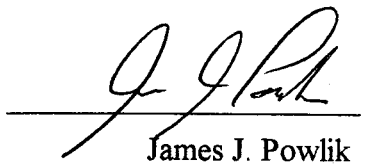
Finally, I thank Úna for ultimately making this manuscript possible. To this day, she is greatly missed.



James J. Powlik

PUBLICATION OF THESIS RESULTS

Portions of this dissertation are currently in press or under review for publication. As of this writing, the status and authorship of these manuscripts is as follows:

Chapter 1 - portions of Chapter 1 (habitat characters) have been submitted to the *Journal of Plankton Research* (U.K. - D. H. Cushing, editor) as:

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A. G. Lewis is included as second author of this manuscript as the research supervisor of the candidate. The manuscript itself was entirely compiled, written and edited by the candidate, who is listed as the senior author.

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(continued)

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A. G. Lewis is included as second author of this manuscript as the research supervisor of the candidate. M. Spaeth advised on the preparation of slides and culture maintenance, and provided several illustrations used as reference to the text material. The manuscript itself was entirely compiled and written by the candidate, who is listed as the senior author.

Chapter 5 - portions of Chapter 5 (population data) have been submitted to the *Journal of Plankton Research* (U.K. - D. H. Cushing, editor) as part of the manuscript indicated under Chapter 1 above.

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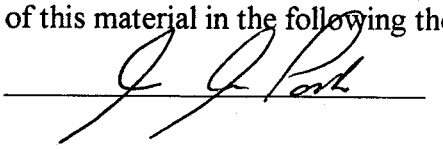

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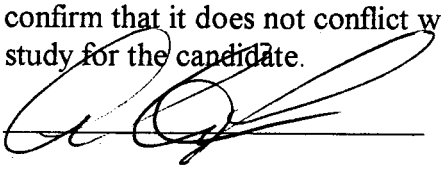

Alan G. Lewis

16 March, 1996

The University of British Columbia

Dedicated to Diana, Goddess of the tides.
Thank you for letting me explore, and play awhile in your back yard.
And for letting me live.

Also dedicated in memory of Mr. John D. G. Boom,
nearly as responsible for the completion of this thesis as its author.
And to whom Diana was far less forgiving.

INTRODUCTION

"A bird can roost but on one branch.
A mouse can drink but its fill from a river."

— CHINESE PROVERB

Since the inception of the discipline, the acicular yet deceptively simple observation that "no species lives everywhere" has been a fundamental impetus for the study of ecology. Through empirical manipulative and mensurative study, community structure and the interactions among their constituents have been investigated in terms of niche breadth (MacArthur, 1968; Colwell and Futuyma, 1971), biotic and abiotic disturbance (Dayton, 1971; Woodin, 1978; Sousa, 1979), species diversity and competition (Connell, 1961, 1972; Menge, 1976; Connell, 1978; Underwood, 1981; Bengtsson, 1986), herbivory or predation (Menge, 1976; Lubchenko, 1978; Coull and Wells, 1983; Valiela, 1984), to list only a few representative studies. The littoral zone of marine and estuarine ecosystems has been compared to tropical rainforests and coral reefs in terms of species diversity and habitat complexity, and perhaps even surpasses those comparisons when considered as the interface between two fluid media of vastly different physical properties. Among all varieties of ecosystem, the rocky intertidal zone demonstrates a uniquely intimate and complex association between biota and the habitat they occupy.

A number of studies have sought to designate and differentiate intertidal pools, using a variety of criteria, including: frequency of tidal flushing (Igarashi, 1959), macroflora (Kain, 1958; Gustavsson, 1972; Dethier, 1984), diatoms (Metaxas and Lewis, 1992), copepods (Fraser, 1936a), and fish (Green, 1971; Mgaya, 1992). Other examples are provided in the review of Metaxas and Scheibling (1993), including the observation of

Underwood (1981) that littoral pools may not even be considered true intertidal habitats, since the organisms within them remain immersed following the tide's ebb.

Despite the ease of shoreline access, discrete volume and comparative isolation of these "aquaria by the sea" as vessels for the study of microscale ecological processes, the interactions within littoral and supralittoral pools can compare in complexity to that of much larger ecosystems. Metaxas and Scheibling (1993) caution that care must be taken in selecting 'replicates' among tidal pools, since differences in elevation, exposure to wave splash, pool volume, shading, allochthonous debris, geochemistry, or fresh water influx can vary substantively, even among pools a only few meters apart. Ganning (B., 1971), Green (1971), and Morris and Taylor (1983) are among numerous studies documenting the physico-chemical conditions in intertidal pools; thermal or haline stratification, oxygen, pH, and carbon dioxide can vary widely among pools or within a single pool, and may fluctuate on an hourly basis, depending on the pool size, volume, atmospheric conditions and biological activity. Markedly different habitat characters can also be expected based on the frequency of tidal immersion of the pool, and whether it is considered a sublittoral, littoral, or supralittoral habitat.

THE SUPRALITTORAL ZONE

The current thesis uses the definition of Kozloff (1983, p. 198), which marks the lower limit of the supralittoral fringe at 1.8 m above mean lowest low water (MLLW or 0.0 m) in California and 2.1 to 2.4 m in Washington and on Vancouver Island. This discrepancy is due to the increased amplitude of the tides; at more northerly latitudes along the Pacific coast of North America, highest tides may reach 3.7 m, compared to tidal maxima of 2.5 m in central and northern California. I will also use the definitions of Metaxas and Scheibling (1993) to distinguish between *tide pools* (large volume water deposits experiencing regular or semi-regular flushing by tidal activity), *rockpools* (small water deposits associated with fresh water systems), and *splashpools* (small sea water

deposits of higher elevation, hence isolated from regular tidal influence), with the latter term being most applicable to the current study. As will be discussed, supralittoral splashpools are quite distinct from the larger, bowl-shaped tide pools found lower in the littoral zone, carpeted with algal crusts and anemones and home to much more abundant and diverse assemblages of motile organisms; the image of the "typical" tide pool.

Supralittoral pools may be replenished with sea water only by wave splash, waves associated with storm events, and the highest tide conditions, which may be extant only one or two days per tidal cycle (Egloff, 1966; Dybdahl, 1994). Indeed, given the comparatively high shoreline position and smaller volume of these pools, organisms within them may be impacted more significantly by atmospheric than oceanographic conditions. Whether to designate pools as emergent or semi-emergent substrata is certainly less in question for supralittoral pools, which may evaporate completely within a few days or even a few hours, only to be flooded anew by wave activity or runoff.

Within habitats, patterns of organism distribution can be attributed to physical, biological, and chemical factors. The magnitude and influence of each of these will vary according to location, season, and the innate tolerance and resilience of the organisms considered. The influences particularly applicable to supralittoral meiofauna are summarized briefly below.

Physical Influences: Among sessile or encrusting organisms, disturbance of the rocky intertidal zone (as by log strikes or exposure to waves) serves to open new areas for recruitment and colonization, and checks the monopolization of space by competitively dominant organisms (e.g., Dayton , 1971; Sousa, 1979; Paine and Levin, 1981). Among other abiotic influences, fluid circulation is an effective influence in the active or passive redistribution of organisms, particularly small or planktonic life-history stages, and supralittoral pools may be equally influenced by atmospheric circulation (wind, intense precipitation) as by oceanographic processes (wave splash, longshore transport). Among

rockpool Crustacea, Brown and Gibson (1983) provide the example of dormant egg stages of the brine shrimp *Artemia,* redistributed by wind following the evaporation of rockpools. Igarashi (1959) similarly found an inverse relationship between the frequency of tidal inundation and the age and stability of *Tigriopus japonicus*. Fraser (1936a) included physical influences among the explanation for his observation that the diversity of copepod species on rocky shores was highest at intermediate elevations, but copepod *density* was highest in largely monospecific populations of *Tigriopus fulvus* entrenched in hospitable supralittoral pools.

Biological Influences: Competitive interaction for space is the predominant biological process structuring rocky shore communities (e.g., Connell, 1961; Menge, 1976; Underwood, 1981). The characteristic patterns of zonation observed on rocky shores is often established by the physiological tolerances of the organisms involved, notably benthic meio- and macrofauna (recent examples include Dethier, 1982; Huggett and Griffiths, 1986; Kooistra et al., 1989; Metaxas and Scheibling, 1993). In isolated, small volume supralittoral pools, microscale processes including respiration, photosynthesis, and bacterial activity may more significantly determine the immediate conditions of the pool (Morris and Taylor, 1983). Higher on the shore, anthropogenic inputs, or nitrification from guano or the excreta of shoreline vertebrates may also affect biological activity within pools (e.g., Ganning and Wulff, 1969), while organic debris deposited by storm activity may alter significantly the detrital material available for reduction by bacteria.

Chemical Influences: Chemical signaling in crustacea has been discussed by Katona (1973) for *Eurytemora affinis* and *E. herdmani*; by Griffith and Frost (1976) for *Calanus pacificus* and *Pseudocalanus* sp.; and by Gleeson et al. (1987) for *Pseudodiaptomus coronatus*. Bozic (1975) experimentally described an "aggregation pheromone" in *Tigriopus* (I assume *fulvus*), and Lazzaretto et al. (1990) proposed a similar species-specific agent in the congeners *T. fulvus*, *T. californicus* and *T. brevicornis* that

allowed the copepods to locate previously inhabited vessels. These authors further suggested that the small size and (they assumed) poor sensory development of copepods may lead to their reliance on chemical signaling; Dethier (1980) suggested that *Tigriopus* (*californicus*) may even use such chemical emissions to relocate to previously-colonized pools following wash out by wave splash. Suspended in the water column, however, I submit that the ability of the copepods to detect or respond to such stimuli under dynamic, wave-washed conditions may be significantly constrained.

THE GENUS *TIGRIOPUS*

There are approximately 2800 described species within the order Harpacticoida, one of seven divisions of the class Crustacea, subclass Copepoda. The genus *Tigriopus* Norman 1868 is one of 9 genera and 80 species within the family Harpacticidae, itself one of 34 families of the Harpacticoida. Of these 34 families, 17 encompass 93% of the genera and 88% of the species (Coull, 1982). Currently, there are seven recognized species within the genus *Tigriopus*, consisting predominantly of Pacific species *Tigriopus californicus* (Baker 1912) and *T. japonicus* Mori 1938, and the Atlantic/Mediterranean species *T. brevicornis* (O. F. Müller 1776), *T. fulvus* (Fischer 1860) and *T. minutus* Bozic 1960. Congeners in the southern hemisphere include *T. angulatus* Lang 1933 and *T. raki* (Bradford 1967) from records in New Zealand, and several varieties of *Tigriopus* have been reported, particularly in the European literature. Monk (1941) is generally attributed with establishing the taxonomy of *T. californicus*, which had been reported previously as *Tisbe californica* (Baker, 1912) and *Tigriopus triangulus* (Campbell, 1930).

Over the past four decades, a legion of studies have used *Tigriopus* congeners for a wide variety of laboratory studies. Experimental use of *T. californicus* alone includes studies in feeding and nutrition (Provasoli et al., 1959; Lear and Oppenheimer, 1962; Anderson and Stephens, 1969), sex determination (Vacquier, 1962; Vacquier and Belser, 1965), tolerance to thermal or haline shock (Ranade, 1957; Huizinga, 1971; Kontogiannis,

1973), osmoregulation and physiology (McDonough and Stiffler, 1981; Goolish and Burton, 1988, 1989), reproduction (Burton, 1985), genetics (Ar-rushdi, 1958; Battaglia et al., 1978; Burton and Feldman, 1981; Burton and Swisher, 1984; Burton, 1990; Brown, 1991), evolution (Burton, 1986; Palmer et al., 1993), histology (Sullivan and Bisalputra, 1980), use as bioassay organisms (Syvitski and Lewis, 1980; Shaw, 1994), tolerance to pollutants (Kontogiannis and Barnett, 1973; O'Brien et al., 1988), and suitability as a food source for fish stocks (Morris, 1956; Fahey, 1964). While a discussion of all such applications is beyond the scope of the current thesis, studies addressing the field ecology of *Tigriopus* species are far less numerous, and will be discussed in Chapter 1.

Conclusive morphological or behavioral distinctions have not been established, and experimental comparisons between species (Battaglia et al., 1978; Lazzaretto et al., 1990) or distant populations of the same species (Burton, 1990, for *T. californicus*) appear to at least produce viable F1 progeny. As will be discussed in later chapters, all *Tigriopus* congeners demonstrate a high resilience to changes in temperature and salinity (Ranade, 1957; Huizinga, 1971; Kontogiannis, 1973), and resistance to anoxic or polluted conditions (Fraser, 1935; Kontogiannis and Barnett, 1973; O'Brien, 1988). Indeed, much of the "speciation" among *Tigriopus* congeners has been based on little more than the zoogeography of the organism or minute differences in morphology; a comprehensive evaluation of inter-specific reproductive compatibility among *Tigriopus* congeners has not been published (but see Bozic, 1960; Lazzaretto et al., 1990).

Distribution of Tigriopus *Congeners:* Published accounts of the geographic range of *Tigriopus* species are notoriously anecdotal or vague in their description, and details of the *in situ* habitat conditions and collection methods used are often abbreviated in published reports. Belser (1959, p. 58) describes *Tigriopus* as a nearly ubiquitous inhabitant of rocky shorelines, "bordering every ocean of the world," but this assertion is probably generous. Obviously, any described range refers only to the areas within which a

given species has been collected and correctly identified. Further, the mere occurrence of an organism in a given region does not provide evidence that the organism is adequately exploiting the resources of this habitat, nor sustaining itself within it.

Tigriopus californicus is typically described as occurring from Baja, California, to Alaska, along the Pacific coast of North America (Belser, 1959; Dethier, 1980). The range of *T. brevicornis* is generally taken to be the northeast Atlantic coast of Europe, including the British Isles (Clark, 1968; Harris, 1973), Iceland, Norway, Normandy, Monaco and Spain (Belser, 1959). Belser (1959) and Bozic (1960) describe the range for what is presumably the conspecifics *T. fulvus* and *T. minutus* as the Bay of Naples eastward into the Adriatic Sea. Bradford (1967) clarified descriptions of *T. angulatus* in New Zealand from records of *T. californicus* (and possibly *Harpacticus brevicornis* as far south as the Antarctic Peninsula), and provided an account of a second congener in the southern hemisphere, *Tigriopus raki*.

THE EFFECT OF HABITAT

For short-lived organisms, variability in resource selection and life-history parameters may act to provide a greater 'bet hedging' against environmental fluctuations (Jain, 1979). As suggested by Bryant (1974) for *Drosophila*, as much as 70% of geographic variation in heterozygosity could be produced by fluctuation in environmental variables. By extension to the "marine fruit fly" *Tigriopus californicus*, it is not surprising that the organism exhibits such an apparently high degree of plasticity in its tolerance to physical extremes and fluctuations in environmental conditions. Given the minute size of the organism against the highly dynamic and irregular features of the rocky intertidal shore,

it is also not surprising that there is such an apparent restriction in gene flow between *Tigriopus* metapopulations[1] (discussed in Burton, 1986; Brown, 1991).

The question therefore remains: to what extent has *T. californicus* exploited its comparatively empty high-tide niche, and to what extent is it limited from other areas? Despite the popularity of the genus as the subject of scientific study, comparatively few studies have clearly defined the conditions under which the organism thrives *in situ*, the extent of its endemic range, and the agents that act to restrict or extend these parameters.

The influence of these agents of dispersal may not be incidental to interpret and explain the observed distribution of *Tigriopus* congeners throughout the world, but this aspect of the organism's natural history has not been previously described, nor fully tested. While the current thesis also does not test experimentally the influence of the various abiotic and biotic dispersal agents available to *T. californicus* in Barkley Sound, it does provide a list of such agents, and a discussion of their potentiality (see Chapter 1).

THESIS OBJECTIVES AND PRESENTATION

Using the habitat and population flux of *T. californicus* as specific exemplars, this thesis will detail several aspects of the supralittoral community within the context of the following four objectives:

1. To describe quantitatively the seasonal habitat characters of *T. californicus* in Barkley Sound, the distribution of the copepod within this habitat, and the potential *in situ* flux of the immediate environmental parameters. Clearly such a description is essential to place into proper context the conditions and results of both laboratory and field experimentation, yet a satisfactory account of the organism's supralittoral habitat has not previously been published.

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[1] *Sensu* Gilpin and Hanski (1991), a *metapopulation* is a collection of local populations linked by dispersal. As used by Dybdahl (1994), such an assemblage may also be subject to frequent extinction events.

2. To elucidate the mechanisms by which *T. californicus* resists the effects of exposure in ephemeral splashpools, including the co-incidence of vegetation (Chapter 2), and the ability of the organism itself to resist desiccation (Chapter 3). While macrofauna may provide either refugia or a surface for the growth of nutritive microflora for *T. californicus*, the genera of seaweeds and patterns of co-incidence or exclusion in *T. californicus* pools have not been established. Secondarily, while accounts of the organism's response (as to pollutants or physiological tolerance) has been broadly established under experimental conditions, few of these experiments have been conducted under conditions truly representative of supralittoral splashpools.
3. To discuss the potential of several dispersal agents to produce the observed distribution of *Tigriopus* species. As an organism with the innate physiological tolerance to live anywhere in the littoral zone, why is the organism apparently 'restricted' to supralittoral pools? And if so constrained, why is the global distribution of the genus so ubiquitous in temperate splashpools? A listing of such agents, related to the supralittoral habitat and considerate of the copepod's innate tolerance, has also not previously been published.
4. To describe the development of *T. californicus* and offer revised parameters for estimating the flux of *T. californicus* populations. Although a number of studies have discussed the generation time and fecundity of laboratory cultures of *Tigriopus* species (e.g., Huizinga, 1971; Burton, 1985; Kahan et al., 1988), a clear description of the life-history of *T. californicus* based on *in situ* observations and the environmental considerations introduced above is not currently available.

The thesis proposes to address the above objectives within the context of a series of mensurative and manipulative studies. These findings will be presented in the following order:

1. A quantified description of the supralittoral habitat of *T. californicus* in Barkley Sound, including the predominant shoreline conditions, seasonal flora and fauna, and basic water conditions. A census of biotic and abiotic agents that may act to cull or redistribute the copepod is also provided (Chapter 1);
2. An experimental analysis of processes that occur within isolated pools, specifically the observed association of *T. californicus* with certain predominant macroalgae (Chapter 2), and the copepod's innate resistance to desiccation during intervals of complete or nearly complete evaporation (Chapter 3);
3. An unprecedented description of *T. californicus*' development in laboratory culture, and notably, under temperature and salinity regimes truly representative of *in situ* conditions (Chapter 4); and
4. Presentation of data on the population density and age structure within *T. californicus* pools throughout the year. Finally, based on the observations in Chapters 1 through 4, an attempt is made to estimate the growth, decline, and frequency of extinction for *T. californicus* populations over approximately a single generation (Chapter 5).

In following these objectives, and sequence of presentation, the current thesis will seek to contribute several explanations to the overarching ecological question: why is *Tigriopus californicus* not found "everywhere" among the various aquatic biotopes. The chapters that follow provide a series of field and laboratory experiments that purport, firstly, to define the habitat characters and shore-bound limits of the organism; secondly, to identify the agents which potentially act to restrict or extend this range; and finally, describe the intrinsic ability of the organism to procreate and propagate its numbers within the constraints of its habitat.

CHAPTER 1: HABITAT CHARACTERS OF *TIGRIOPUS CALIFORNICUS* IN BARKLEY SOUND, INCLUDING NOTES ON THE POTENTIAL OF SEVERAL AGENTS FOR THE DISPERSAL OF SPLASHPOOL COPEPODS.

INTRODUCTION

"Whether Tempter sent, or whether tempest tossed thee here ashore,
Desolate yet all undaunted, on this desert land enchanted —"

— EDGAR ALLEN POE, 1845

Since the earliest descriptions of *Tigriopus* copepods (Müller, 1776; Norman, 1868), constituents of this genus have become subjects familiar to a variety of mensurative and manipulative studies in harpacticoid copepod biology (Fraser, 1936a, 1936b; Provasoli et al., 1959; Lear and Oppenheimer, 1962; Huizinga, 1971; Harris, 1973; Battaglia et al., 1978; Dethier, 1980; Burton and Feldman, 1981; Kahan et al., 1988). From Belser (1959), *Tigriopus* copepods are found on the supralittoral fringes of nearly every world ocean, including the shores of Japan (*Tigriopus japonicus*), Northern Europe (*T. brevicornis*), the Adriatic (*T. fulvus* and *T. brevicornis*), and North America (*T. californicus*).

The Habitat of *Tigriopus* Copepods

Despite being heralded as an oceanic "white rat" (Belser, 1959) or "marine fruit fly" (Dethier, 1980) for their innate physical tolerance and ease of culture in laboratory study, substantive field studies of *Tigriopus* spp. are few in number (Table 1.1). Uniformly, these studies omit critical details of the habitat in which the organism lives; in laboratory studies, methods of copepod collection are similarly abbreviated, and

TABLE 1.1. Representative studies of *Tigriopus* field populations and their location.

Tigriopus californicus		**Other *Tigriopus* species**	
Study	**Location**	**Study**	**Location**
Baker, 1912	Laguna Beach, California	*T. fulvus*	
		Fraser, 1936a,b	Port St. Mary, U.K.
Monk, 1941	(California)	Bozic, 1960	(Europe)
Egloff, 1966	Mussel Grove, California	Carli et al., 1984	(Spain)
Vittor, 1971	Charleston, Oregon		
Dethier, 1980	San Juan Island, Washington	*T. brevicornis*	
		Comita and Comita, 1966 (samples from)	Isle of Cumbrae, Scotland
Burton et al., 1979	Bodega Bay, Moss Beach, California	Clark, 1968	(British Isles)
		Harris, 1973	Plymouth, U.K.
Burton and Feldman, 1981	Los Angeles, California		
Dybdahl, 1989	Bodega Bay, California		
Brown, 1991	Bodega Bay, California	*T. japonicus*	
		Igarashi, 1959, 1960	(Japan)
Dybdahl, 1994	Bodega Bay, California	Koga, 1970	Fukuoka, Japan
	San Juan Island, Washington	Takano, 1971	Sagami Bay, Japan
Powlik and Lewis (current and in press)	Barkley Sound, British Columbia		

considered extraneous to the subsequent use of the cultured organism. Studies of *in situ* conditions have included discussions of population age and stability with tidal influence (Igarashi, 1959), sex ratio (Egloff, 1966), adaptive strategy (Vittor, 1971), the influence of predation (Dethier, 1980) and metapopulation dynamics (Dybdahl, 1994). *Tigriopus* spp. are routinely described as 'restricted' to the supralittoral zone of rocky shores (2.4 to 4.1 m above lowest normal tide, *sensu* Kozloff, 1983). A typical habitat description is here excerpted from Lear and Oppenheimer (1962, p. lxiii):

> "*Tigriopus californicus* grows only... in pools above the high-tide mark and dependent upon splash for sea-water replenishment. This environment is characterized by extreme fluctuations of temperature and salinity with occasional desiccation. The *T. californicus* used were collected from splash pools on a shelf rock, a large shale formation along the foot of the cliffs..."

As a short-lived organism (egg to C-VI adult stage in approximately 21 days at 20°C (see Chapter 4), *T. californicus* may be particularly susceptible to fluctuations in its environment. *Tigriopus californicus* is often described as a generalist feeder (Vittor, 1971; Dethier, 1980), tolerant to a wide range of salinity (normal activity observed from 0 to 80‰) and temperatures (in excess of 30°C, including sudden changes of 10°C or more) (Huizinga, 1971; Kontogiannis, 1973). Hence, as an organism that *could* ostensibly live anywhere in the intertidal zone, it is particularly illustrative to ask why *T. californicus* and the congeners and variants of the genus do not.

Tide pools, estuaries and other geographically-isolated coastal areas provide a proving ground for certain relationships between genetics and ecology "at a micro-geographical level" (Battaglia et al., 1978, p. 53), and with the provision of a fluid medium may even surpass isolated terrestrial systems in this regard. Igarashi (1959) describes an inverse correlation of stable *Tigriopus* (I assume *japonicus*) populations with frequency of tidal inundation . Vittor (1971) finds a high degree of variability (and proposes plasticity) in the fitness traits of *T. californicus* populations continuously

exposed to the highly fluctuating temperatures and salinity of the supralittoral zone. Mechanisms for transport between exposed pools are limited, and accordingly, Burton and Feldman (1981) and Brown (1991) find a significant constriction in gene flow between *T. californicus* populations even those separated by only a few meters.

While wave-washed shores can provide a formidable challenge to empirical sampling, the exposed water deposits containing *T. californicus* are generally barren, small in size, and may be isolated from the sea for several days without evaporating or being replenished. This not only facilitates access to field sites, but provides natural vessels in which to study changes in chemical and physical properties (e.g., Morris and Taylor, 1983) as well as short-term population response (Vittor, 1971; Dethier, 1980; Dybdahl, 1994).

Agents of Dispersal for Splashpool Copepods

Tigriopus species are nearly ubiquitous on temperate rocky shores, and are commonly described as "restricted" to supralittoral splashpools from 2 to 5 m above mean water level, depending on the degree of exposure. These ephemeral water deposits, often isolated from sea water replenishment for several days, may freeze in winter, evaporate in summer, flood from precipitation and runoff, and accumulate allochthonous shore debris. Given the ostensible similarity and widespread occurrence of *Tigriopus* congeners in barren, short-lived water deposits, how then can the organism still be considered isolated in these habitats?

There exists a remarkable homozygosity within pools or *Tigriopus californicus* metapopulations, yet Burton (1986, 1990) and Brown (1991) found populations of *T. californicus* to be genetically heterogenous between individual outcrops, ostensibly contradicting the high capacity for dispersal commonly accredited to the organism (e.g., Burton, 1986). On the basis of gene loci, Burton and Feldman (1981) found gene flow between inhabited outcrops to be significantly constricted. Burton and Swisher (1984)

reported evidence of exchange of genetic material between pools within patches of *T. californicus* habitation, while Brown (1991) found a high cost associated with individual pairings beyond the parameters of a single pool. Actively or passively, what means of dispersal or recovery does it potentially utilize to maintain its position and so successfully colonize temperate rocky shores?

The term *dispersal agent* is used here in lieu of *colonization vector*; the former term emphasizing a means of transport away from the point of origin, but not assuming the subsequent founding of a population by the organism so dispersed. Broadly, such agents may be designated as: 1) abiotic agents, including wind, waves, and current activity; 2) short-distance biotic agents, providing dispersal over a limited area; and 3) long-distance biotic agents, providing widespread or even global dispersal over time. Acting in concert with any of these agents are the behavior of the organism, as well as its physiological tolerance and acclimation to sudden or gradual changes in habitat or climate. The magnitude and influence of all these agents is additionally subject to temporal and seasonal variation.

The current chapter proposes to detail the conditions extant in supralittoral pools containing *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. In addition, it will present a non-experimental review and discussion of several ambient agents for dispersal, which may act to redistribute *T. californicus* individuals between isolated pools.

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 centered at Lat. 50°N; Long. 125°10'W, see Figure 1.1). From this initial census, 85 pools were selected using stratified random sampling and monitored for the remainder of the study. Sampling intervals one to two 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. When conditions permitted, additional pools found to contain *T. californicus* were also surveyed for biotic and abiotic features, providing the *n* values listed in Tables 1.2 and 1.3.

Each pool was mapped according to:

1. tidal elevation, determined relative to landmarks of known elevation, local tide tables (DFO, 1995; Canadian Coast Guard, Bamfield Detachment, pers. comm.; N.J. Wilimovsky, pers comm.), and repeated measure from the waterline using an inclinometer (*sensu* Kain, 1958);
2. pool dimensions and volume, determined using a meter stick and 1 m^2 quadrat;
3. taxa and percent-cover of macroalgae (*sensu* Dethier, 1982);
4. abundance of zoobenthos, using a 10 cm^2 quadrat; and
5. fundamental water conditions, including salinity, temperature, oxygen concentration and hydrogen ion concentration. Salinity was recorded using a Hanna Model 9033 conductivity meter; temperature using a Fisher field-protected thermometer; and pH using a Fisher Alkacid full-range pH kit.

Abundance of *Tigriopus californicus* (Baker) was also determined; data and analyses of the density, age structure, growth and decay of *T. californicus* populations are presented in Chapters 4 and 5.

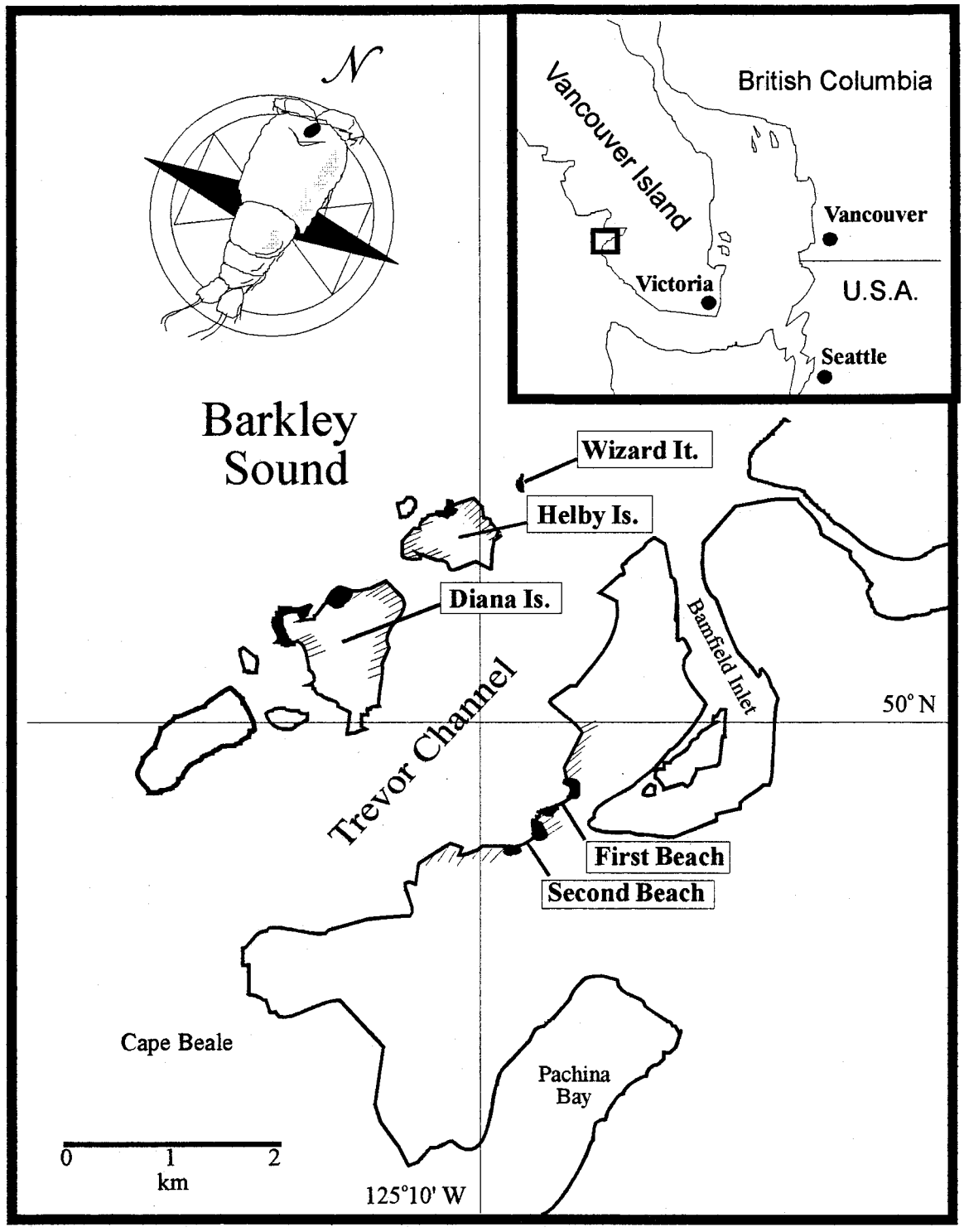

FIGURE 1.1. Area of study. Lined coastline indicates regions surveyed for *Tigriopus californicus* pools; black coastline indicates the location of field sites monitored over the course of study.

RESULTS

The seasonal abundance, abiotic and biotic conditions of *Tigriopus californicus* pools are summarized in Tables 1.2 and 1.3.

Abiotic Conditions: From Table 1.2, 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 1.2). Within this restricted range, populations did not necessarily persist throughout the year for those pools that were monitored regularly (Chapter 5). Sediment in *T. californicus* pools was most prevalent in the spring, but coincided most closely with storm activity and adjacent 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 possibly assists the diffusion of atmospheric oxygen to dense populations of *T. californicus.*

Overall, 90.1% of all *T. californicus* pools were situated between 3.0 and 5.0 m tidal 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 1.2, 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 fresh water in autumn (diluted by precipitation) to 139‰ in at least one isolated summer pool; the annual mean was 30.2 ± 8‰[1]. The range of values observed precluded any calculations of statistical difference and demonstrated a high degree of variation between pools. While irregularities in pH were

[1] Note: the accepted standard for providing salinity is Practical Salunity Units (PSU), which is presented without units. Parts per thousand (‰) is used throughout this manuscript to facilitate comparison with previous (biological) studies, and to remain consistent with the *Instructions to Authors* guidelines for those portions of the thesis that are in press.

TABLE 1.2. 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 Temp. (°C)	Water Temp. (°C)	Salinity (‰)	pH	Oxygen (mg/L)
Autumn *									
mean	2.01	3.9	7.0	4.02	5.6	11.3	27.1	not	not
range	(-0.1 - 3.8)	(2.2 - 6.7)	(0.5 - 69)	(0.09 - 30)	(-1.4 - 11.5)	(6 - 15)	(1 - 36.4)	recorded	recorded
s.e.	1.2	0.8	14	5.8	4.5	1.9	5.6		
n	30	143	143	143	26	143	143		
Winter **									
mean	2.09	3.9	8.9	7.01	5.5	10.7	21.4	7.3	6.8
range	(0 - 3.9)	(1.5 - 6.7)	(.1 - 55)	(0.06 - 5.0)	(-4 - 10)	(7 - 14)	(3.4 - 32)	(6.2 - 8.3)	(3.5 - 10.1)
s.e.	1.3	1.0	17	12.5	5.2	1.3	9.1	0.2	0.9
n	31	114	114	114	21	114	114	42	42
Spring ***									
mean	1.96	3.9	3.8	3.87	17.2	19.3	32.5	7.6	8.1
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)
s.e.	1.2	0.9	13	17.2	6.1	2.9	15.7	0.7	2.3
n	61	184	184	184	24	184	184	45	45
Summer ***									
mean	2.03	3.6	5.2	3.38	15.5	21.8	40.1	7.5	6.2
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)
s.e.	1.9	0.8	67	6.7	7.3	3.2	17.2	0.3	2.5
n	62	312	312	312	34	312	312	39	39

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

TABLE 1.3. Biotic conditions of Barkley Sound splashpools containing *Tigriopus californicus* populations.

	Macroflora (%-cover of)				**Fauna**	
	Enteromorpha spp.	*Scytosiphon* spp.	Encrusting spp. (var.)	Mixed Sediment	% of *Tigriopus* pools containing:	Individuals m^{-2}
Autumn *					Amphipods	4
mean	5.0	0.0	16.1	12.0	Barnacles (*Chthamalus*, *Balanus* spp.)	150
range	(5 - 5)	n/a	(5 - 30)	(5 - 40)	Crabs (*Hemigrapsis* spp.)	0.5
s.e.	n/a	n/a	12.3	15.7	Littorines (*Littorina* spp.)	90
present in	2 of 88	0 of 88	19 of 88	5 of 88	Mites (*Neomolgus* and other spp.)	30
(%)	2.27	0.00	21.60	5.68	Sculpins (*Oligocottus* spp.)	1
					Misc. - *Anthopleura*, *Pisaster*	1
Winter **						
mean	16.8	12.5	5.5	0.0	Littorines (*Littorina* spp.)	65
range	(5 - 30)	(5 - 20)	(5 - 10)	n/a	Nematodes	300
s.e.	10.3	10.6	1.9	n/a	Sculpins (*Oligocottus* spp.)	1
present in	22 of 47	2 of 47	10 of 47	0 of 47		
(%)	46.81	4.26	21.28	0.00		
Spring ***					Amphipods	6
mean	20.9	20.2	26.3	25.0	Barnacles (*Chthamalus*, *Balanus* spp.)	112
range	(5 - 90)	(5 - 70)	(5 - 70)	(10 - 80)	Crabs (*Hemigrapsis* spp.)	0.5
s.e.	21.8	17.8	20.0	21.7	Littorines (*Littorina* spp.)	128
present in	44 of 384	47 of 384	26 of 384	10 of 384	Mites (*Neomolgus* and other spp.)	46
(%)	11.46	12.24	6.77	2.60	Nematodes	190
					Sculpins (*Oligocottus* spp.)	1.5
					Misc. - *Acmaea*, *Pisaster*	1
Summer ***					Amphipods	4
mean	19.6	0.0	5.6	17.0	Barnacles (*Chthamalus*, *Balanus* spp.)	80
range	(5 - 80)	n/a	(5 - 10)	(5 - 40)	Crabs (*Hemigrapsis* spp.)	1
s.e.	23.3	n/a	1.8	12.2	Littorines (*Littorina* spp.)	90
present in	23 of 498	0 of 498	8 of 498	55 of 498	Nematodes	360
(%)	4.62	0.00	1.61	11.04	Ostracods	15
					Misc.	1.5

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

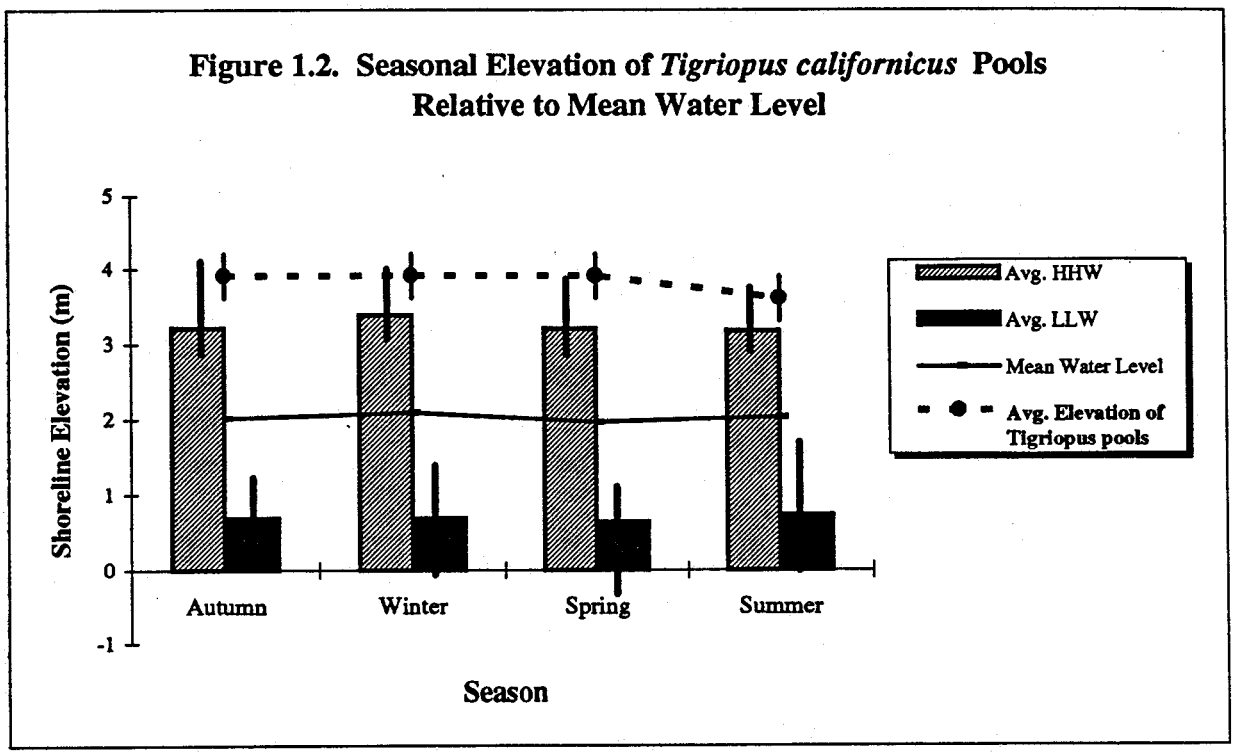

FIGURE 1.2. Seasonal elevation of splashpools containing *Tigriopus californicus* relative to mean water level. Water levels are averaged from local tide tables over sampling intervals in each season. HHW = higher high water; LLW = lower low water from mixed, semi-diurnal tide conditions (DFO, 1995). Error bars on dotted line represent ± 1 standard error; lines on HWL and LLW average bars represent maximum and minimum levels over the study interval.

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: From Table 1.3, splashpools containing *T. californicus* were generally void of macroflora, with the highest co-occurrence of copepods and visible vegetation occurring in winter (24.11% for all species). In summer, only 2.08% of those pools containing *T. californicus* also supported these macroalgae. Overall algal abundance was lowest in the autumn, with the exception of encrusting species, including *Ralfsia* (common name: "tar spot") or a *Ralfsia*-like alga. *Cladophora trichotoma* ("green ball") and *Enteromorpha compressa* ("green confetti") are present throughout the year, but in autumn average 18.3 ± 6.82 and 5 ± 2.27%-coverage, respectively, for all pools surveyed. *Prasiola meridionalis* fringes some higher-elevation pools, especially those nitrified by guano.

In winter, only *Cladophora trichotoma* was found regularly, occupying 30% of the available substratum, though not in those pools containing *T. californicus* (see Chapter 2). *Enteromorpha compressa* coverage averaged 16.8 ± 46.8%, *Scytosiphon lomentaria* averages 12.5 ± 4.26%-cover, hence its *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 percent-cover and genera of encrusting algal mosaics, or sporadic tufts of species such as *Endocladia*, was found to be imprecise.

In spring, the principal seaweeds were *Enteromorpha compressa* (20.9 ± 11.46%) and *Cladophora trichotoma* (36.1 ± 3.65%) , while *Scytosiphon lomentaria* and algal crusts reach their greatest annual abundance. During the highest seasonal abundance, phaeophytic algae and debris may color pools orange or red; *Hildenbrandia* and *Endocladia* spp. often occur apart from other algae, and may become brownish in color 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.

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 percent cover, but much of this material forms large mats of salt-encrusted filaments superficially devoid of chloroplasts. A second species, *E. intestinalis*, occurs more commonly in summer than in spring. *Cladophora trichotoma* persists as the most common macroalgae, averaging 28.8 ± 6.43%-cover in spring, but again, does not usually coincide with *T. californicus* habitation (see Chapter 2).

Dispersal Agents: Fauna common to *T. californicus* pools or the adjacent shoreline are summarized in Table 1.4. Salt water mites, gammaridean amphipods, and littorines (*Littorina* sp.) are most common in the autumn and spring, with barnacles (*Chthamalus* and *Balanus* spp.), limpets (*Acmaea* sp.) and mussels (*Mytilus* spp.) 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 comparatively plentiful and physical conditions are less extreme.

The avifauna of Barkley Sound were considered as potential dispersal agents, but as an *a priori* consideration, could not be collected and examined for the presence of ectoparasites (including copepods) 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, D.C.) were instead inspected (species and specimen numbers listed in Appendix C). Avifauna common to the area include black oystercatchers (*Haematopus bachmani*), turnstones

(*Arenaria* spp.), California gulls (*Larus californicus*), and Glaucous-winged gulls (*L. glaucescens*) (Campbell et al., 1990 and pers. obs.).

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 any *T. californicus*. However, other microcrustaceans (unidentified isopoda and copepoda) and isopods (unidentified spp.) were occasionally found in the plumage of museum specimens of black oystercatcher (*Haematopus bachmani*) and California gull (*Larus californicus*) (identification from specimen tags and Campbell et al., 1993).

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.) forage in the high intertidal zone. Leaf and seaweed debris, insect larvae and allochthonous shore materials are commonly found in the highest *T. californicus* pools.

TABLE 1.4. 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	Long-Distance
Invertebrata					
Anemones (*Anthopleura* spp.)	Anthozoa	X		N/A	
Amphipods (*Traskorchestia* sp.)	Crustacea		X	X	
Barnacles (*Balanus, Chthamalus* spp.)	Crustacea	X		N/A	
Crabs (*Hemigrapsis nudus*)	Crustacea		X	X	
Littorines (*Littorina* sp.)	Gastropoda		X	X	
Limpets (*Acmaea* sp.)	Gastropoda	X		N/A	
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 oystercatchers (*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.
** Longer-distance transport potential on mainland.

DISCUSSION

The following discussion provides a comparative discussion of 1) general characters of splashpools in Barkley Sound, particularly those containing *Tigriopus californicus*; and 2) the potentiality of several dispersal agents, which may serve to redistribute splashpool copepods between inhabited outcrops. This latter consideration was not tested experimentally for the current thesis, but is included in discussion since a thorough consideration of potential dispersal agents and their mechanism for transport is clearly fundamental to the understanding of the copepod's observed distribution.

Habitat Characters

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 fresh water 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 and Oppenheimer, 1962; Harris, 1973). Flattened foreshores, which flood gradually with the incoming tide and immerse pools by several centimeters 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 acting on microcrustaceans swimming above the bottom. Steep shorelines that produce wave splash may also assist the replenishment or re-distribution of supralittoral copepod populations on a single outcrop (see below).

Fraser (1936a) sampled pools ranging in shoreline elevation from -1.33 feet to 12.73 feet (-0.4 m to 3.88 m), the higher extreme occurring 1.5 m above the high-water mark and the only level observed to contain *T. fulvus* (at populations of over 800 individuals $\cdot$ L^{-1}). Dethier (1980) found pools above 2.2 m elevation to contain *T.*

californicus, with a sharp decline in pools occupied by copepods below that level. While the elevation of *T. californicus* will depend on the degree of shoreline exposure and absolute tidal range, Figure 1.2 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 with 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 (Morris and Taylor, 1983; Metaxas and Scheibling, 1993). The typical size of pool basins (4.57 ± 1.65 m^2 surface area; 62.25 ± 22.13 L volume) agrees with the range of values recorded by Fraser (1936a) and Dethier (1980), however shoreline topography and high levels of precipitation may "bleed" several small, neighboring pools into one another, and greatly extends the upper range of these parameters. The surveyed pools reflect this, with the greatest pools sizes occurring at the time of highest precipitation in the area (11.5 mm · day^{-1} in autumn and 11.9 mm · day^{-1} in winter, see Appendix B). Harris (1973) described pools of 20 L volume and 30 cm depth during spring sampling of *T. brevicornis*; Dethier (1980, p. 102) observed *T. californicus* pools to be "usually less than 10 L." Fraser (1936a) recorded pool volumes of 7.5 to 84 L. The values in Table 1.2 range from less than 5 L to over 110 L for some diluted spring pools. Atmospheric conditions, shoreline exposure, and bedrock contours will obviously produce a high degree of variability in this parameter; for the current study, no season produced *T. californicus* pools of significantly different surface area or volume.

The values in Table 1.2 for temperature, salinity, pH, and oxygen lie within the wide range of values for these parameters published by Morris and Taylor (1983) at a comparable latitude. Harris (1973) recorded a salinity range of 30.2 to 35.2‰ and a temperature range of 8 to 23°C for pools containing *T. brevicornis*. Egloff (1966)

reported air temperatures of 9 to 29°C over an 18-month interval to approximate the range of water temperatures, and all published accounts for *in situ* ranges for temperature and salinity (including Table 1.2) fall well within the tolerance recorded for *T. californicus* in laboratory culture (Huizinga, 1971; Kontogiannis, 1973). Unpublished personal observations of other *T. californicus* pools elsewhere in British Columbia, Washington, Oregon, and California have yielded similar results over the described geographic range of this species, and coincide with descriptions of other temperate areas (e.g., Gustavsson, 1972, in Sweden; Fraser, 1936; Clark, 1968; Harris, 1973; and Morris and Taylor, 1983, in the United Kingdom).

Biotic Habitat Characters: In Barkley Sound, the water of splashpools may acquire any number of remarkable colors, including green (from *Tetraselmis* blooms), 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 sulfur production), pink (from *Oxyrrhis* dinophytes) or colorless and transparent (F.J.R. Taylor, pers. comm.). While the occurrence of bacteria and unicellular algae is virtually assured in these pools, identification of the species present is not easy. Further, the culturing process used to identify bacteria species distances this identification from any reliable description of *in situ* conditions. Takano (1971) mentions the 20- to 35-μm long dinophyte *Oxyrrhis marina* Dujardin as occurring naturally in the habitat of *T. japonicus,* but Takano (1968, cited in Takano, 1971, p. 72) found that *Oxyrrhis* "competed against the larvae of the copepod by feeding upon the same food." Reliable accounts of the natural abundance and identity of microbes in *Tigriopus* pools are unavailable, however those species noted to occur in the high intertidal zone express a high degree of seasonality in their occurrence.

Both *Tetraselmis* and *Oxyrrhis* are most abundant in the summer months, and although both may bloom, they do not typically co-occur with each other (F. J. R. Taylor, pers. comm.) Decay and putrefaction of algal debris, and the bacterial activity

promoting this process, have previously been related to *Tigriopus* occurrence (e.g., Fraser, 1936a). Alternately, microflora may assist in the nutrition of *T. californicus* by facilitating the uptake of nutrients across the copepod's exoskeleton (see Anderson and Stephens, 1969; Khalov and Yerokhin, 1971; Carli et al., 1993). Anthropogenic inputs or nitrogen introduction from animal excreta does not appear to enhance *T. californicus* population growth.

With few exceptions (e.g., Fraser, 1936a) co-incident supralittoral macroalgae are not described in the literature on *Tigriopus* species, although Dethier (1980) mentioned algal crusts and opportunistic *Enteromorpha,* a filamentous green macroalgae noted for its ability to grow in the absence of water flow. 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 percent-cover from Table 1.3 concur with those of Fraser (1936b), Gustavsson (1972) , Morris and Taylor (1983) and Dethier (1980) for temperate, supralittoral splashpools.

Among co-occurring fauna, Fraser (1936a) included *Littorina rudis,* ostracods (*Cythene lutea*), *Dactylopusia brevicornis* (Claus), *D. vulgaris* Sars, *Idya furcata* (Baird), *Amphiascus minutus* (Claus), the harpacticoid *Amphiascus minutus*, and *Chironomous* larvae in his field samples of *T. 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 plankton to be up to 99.98% monospecific (*T. fulvus*), in contrast to the highest species diversity, which was found at the mid-littoral level. From the current observations, *T. californicus* pools are largely monospecific, with other species rarely exceeding a few individuals per sample. Incidence of these other species (not identified) also appear to relate to season and the relief of the beach face: spring plankton populations are typically more diverse, while low-relief shores are more likely to contain non-*Tigriopus* specimens. Insects, leaf

debris, and incidental vertebrates are all factors reasonably influencing splashpools of the exposed supralittoral zone.

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, however the predators themselves were similarly distressed by the physical conditions of the pool. The orange coloration and 'jerky' swimming motion of *Tigriopus* may also make them attractive to visually-oriented prey (J. M. Ganning, 1971). Dethier's (1980) study also demonstrated that *T. californicus* can survive in pools lower in the intertidal zone, provided that predators and wave scour are removed. Mussels have been observed to eat copepod larvae, but not adults (K. G. Kopley, pers. comm., cited in Dethier, 1980), and I suggest the same potential in barnacles (*Chthamalus* and *Balanus* spp.).

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 to 6 individuals $\cdot$ 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. The most significant agents responsible for culling established *Tigriopus* populations may then be predominately cannibalism, desiccation and wave-wash (but see below, and chapters 2 and 3).

Burton and Feldman (1981) suggested that, while complete extinction of *Tigriopus* populations is unlikely, regular depletion of populations may occur, either due to wave activity or seasonal changes in climate and water properties. Dybdahl (1994) considered *T. californicus* pools on the same rock outcrop as forming a *metapopulation*: a collection of local populations experiencing periodic extinction and re-colonization, which is especially characteristic of subdivided or fragmented habitats. He further reported extinction of *T. californicus* populations in 35% of his study pools over a period

of six to eight weeks. On occasion, I have discovered pools in which *T. californicus* which were nearly all apparently deceased. Temperature and salinity were not anomalous in these pools (within the limited time frame 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 (Chapter 3).

Egloff (1966) suggested that summer populations of *Tigriopus californicus* are influenced less by storm activity and wave splash. While wave conditions may be less extreme in the summer, I suggest the influence of evaporation and stagnation may become much more pronounced, particularly in warmer climates. Further, 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 re-hydration (Chapter 3). Hence, in comparing the conditions of *Tigriopus*-inhabited pools, parity of season and latitude between study sites are essential considerations.

Dispersal Agents

Informal observations of *Tigriopus californicus* pools in other areas of British Columbia, Washington, Oregon, and California have indicated similar conditions over much of the described geographic range of this species. While favoring *T. californicus*, the following discussion may be applied to all *Tigriopus* habitats at a comparable latitude.

Abiotic Agents

Hydrochory: The action of waves and currents on exposed, rocky shores must be considered as a principal mechanism for re-distributing *T. californicus*. Igarashi (1959) found a correlation between *Tigriopus* (I assume *japonicus*) population stability and the intertidal elevation of inhabited pools. In his study, no *Tigriopus* were found in pools

routinely flooded at high tide; older populations of varying density were found in high, isolated pools, and younger, less dense populations described at intermediate levels.

For those pools inundated least frequently by tide or wave activity, *Tigriopus* populations may be more significantly influenced by precipitation and drought (Igarashi, 1959). The position of the pools in the current study (1.9 ± 0.3 m above the average water level and 0.8 ± 0.1 m above higher high water levels) suggests that wave splash may act significantly in the replenishment of *T. californicus* metapopulations, and supports the findings of Burton and Swisher (1984), that at least some transfer of individuals may occur between adjacent pools. Runoff, particularly from heavy rainfall, may wash copepods downslope into larger pools, however, although I have found *T. californicus* in shallow crevices or on moistened surfaces between pools, it is not typical for the lower of 'stepped' pools to collect *T. californicus* washed from pools of a higher elevation.

Regular inshore transport by flood tides should also be considered a significant influence (Igarashi, 1959; Vittor, 1971), but primarily for those pools located at a lower tidal elevation and therefore more frequently flushed. R. Burnett (pers. comm. cited in Morris et al., 1980) finds pool populations of vital-stained *T. californicus* to undergo an exchange of nearly half their numbers after a few days, although the net abundance of individuals in the pools changes 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 by wave splash; 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 the water column long enough to colonize adjacent shores. As an exotic or unfamiliar species to either offshore or soft-bottom plankton communities, the 'absence' of *T. californicus* from such samples may often be a case of overlooked or

misidentified specimens. However, if indeed present in these locations, *Tigriopus* copepods clearly do not bloom there to the extent they do in splashpools.

Given the broad geographic range of *T. californicus* (Baja, California, to 58°20' N, *sensu* Belser, 1959; Dethier, 1980), longshore transport should also be considered as a potential dispersal agent, and the major surface currents of the NE Pacific Ocean are illustrated in Figure 1.3. Northward offshore transport by the Alaska Current, southward transport by the California Current, or the opposing inshore circulation of the Davidson Current are immediately apparent mechanisms for the transport of *T. californicus* along the Pacific shore of North America. However, were longshore transport a substantive means of dispersal between colonized areas, *T. californicus* should be commonly deposited in sedimented coastal areas, as well as in plankton hauls or benthic samples from stations adjacent to or located between inhabited rocky shores.

Although it is a common occurrence for *T. californicus* individuals or even entire populations to be displaced from supralittoral pools by wave splash or a flood of precipitation, it is likely that the fate of most of these copepods is to be washed back onto the shore by the subsequent onshore wave action, or to be culled by visually-oriented predators in the open sea. Additionally, *T. californicus* is not a particularly strong swimmer, even in motionless aquaria. The copepod appears to fatigue quickly in its swimming (casual observations of cultures in 25 L vessels), and prefers to occupy the bottom of the vessel. Under low-energy or stagnant conditions, the argument might be made that, whether from fatigue or active downward swimming, the organism would settle into the lower portion of the extant water column, could be carried downshore and ultimately transported along the shore by deep water currents. But again, if the copepod is transported along the shore between locales by waves, surface or bottom currents, this does not account for the organism's absence from sedimented areas between rocky outcrops. Vittor (1971) reported finding no *T. californicus* in plankton hauls immediately offshore of inhabited outcrops, nor have I had success in identifying the

organism in net hauls from offshore the field sites in Barkley Sound. This does not suggest the organism is *not* found in coastal ocean currents, but only that its presence is as-yet undetectable. In addition, dipnet or SCOR net sampling along high-energy rocky shores does not produce satisfactory results[2] (see General Discussion).

Wind: Microcrustacea from estuarine areas, lakes or salt water pools may persist in evaporated basins as encysted eggs, to be passively dispersed by wind (Brown and Gibson, 1983), and *T. californicus* may be similarly re-hydrated from virtually all life stages, including the gravid female (Chapter 3). This observation not only allows the copepod to endure transport, as by wind or avifauna, but also retains the ability of the copepod to produce a viable population almost immediately once delivered to a suitable habitat, and without requiring a mate for insemination once there. It is not uncommon, particularly in summer, for *T. californicus* pools to evaporate completely, exposing the copepods in the bottom of their pool at a density of several thousand individuals per liter (Chapter 3). By extension, it is possible that desiccated *T. californicus* waifs are dispersed by wind, and potentially carried to a hospitable pool or a region of the shore receiving more immediate moisture replenishment (within 5-7 days, from Chapter 3).

Short-Distance Biotic Agents

Supralittoral Fauna: Invertebrate macrofauna in supralittoral pools is often sparse, particularly in the summer, when desiccation and evaporation within this zone is intense. In lower pools, mussels may filter *T. californicus* nauplii from suspension (K. G. Kopley, pers. comm., cited in Dethier, 1980, p. 102). The same might be assumed for larger barnacles (*Balanus* spp.), but has not been demonstrated *in situ*. The motility of littorines and amphipods provides a (slightly) more motile means of transport, but

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[2] Alternate means of sampling microcrustacea from such areas, including the use of mounted plankton traps, was not possible during the time available for sampling.

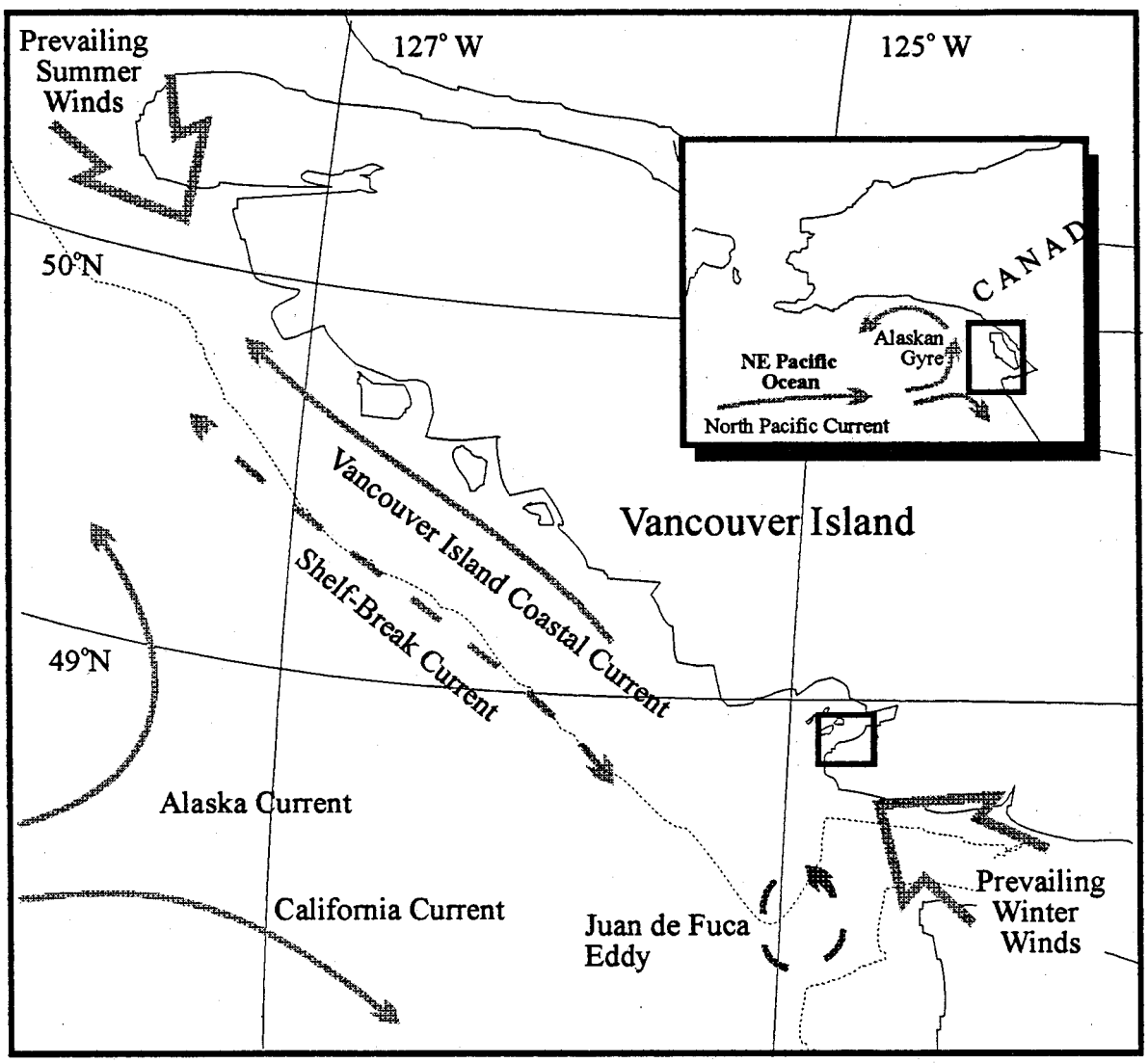

FIGURE 1.3. Current patterns of the NE Pacific Ocean. Generated by wind, the divergence of the North Pacific Current as it reaches the coast of North America moves slightly northward, from 45°N Latitude in winter to 50°N Latitude in summer (Pickard and Emery, 1982). The Shelf-Break Current reverses direction according to the prevailing seasonal winds, and follows the 200 m isobath (approximately indicated by dotted line). In winter, the Vancouver Island Coastal Current (VICC) is driven by the prevailing winds as a northward extension of the Davidson Current; in spring, the transition in wind direction generates the cyclonic Juan de Fuca Eddy. Square on thumbnail map indicates area enlarged; square on enlarged map indicates study area. Illustration derived from Thomson (1981) and Thomson et al. (1989).

these would presumably still be restricted to a very small area of the shore, perhaps even to a single pool.

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 and Feldman, 1981; Dybdahl, 1994), without any conclusive evidence in support of this mechanism. From the calculations of Vittor (1971) and Dybdahl (1994), the transport of a small number (eight to 10) of a variety of life-history stages could potentially re-populate a pool. In the Barkley Sound pools, *Hemigrapsis nudus* is the only crab found consistently in *T. californicus* pools; I know of no published "home range" for the species, 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.

Dethier (1980) proposed predation by cottids and anemones as a major influence 'restricting' *T. californicus* occurrence lower in the intertidal zone. Ganning (J. M., 1971) suggested the orange coloration and erratic swimming style of the organism makes it particularly susceptible to visually-oriented predators, and Burton and Feldman (1981) concur that predation as well as organism behavior may reduce the number of individuals transgressing established metapopulations. Although the influence of predators is curtailed *in situ* by the extreme physical conditions in supralittoral pools, I have observed anemones as well as sculpins in some *T. californicus* pools. From Green

(1971), *Oligocottus* and other sculpins in the high intertidal possess home ranges, enhancing the likelihood of localized *T. californicus* exchange by sculpins or other inshore fishes, but not to an appreciable extent downslope or along the shore.

Mink and deer are also commonly observed to traverse the Barkley Sound field sites, and may incidentally collect *T. californicus* on their appendages or pelts. Otters and sea lions are not observed at the same tidal elevation as most *T. californicus* pools in this study, but might be considered as incidental vertebrates in other field sites. Additionally, while incidental vertebrates may disturb quiescent pools in passing, eutrophication or nitrification from animal excreta does not appear to enhance *T. californicus* population growth (*cf.* Ganning and Wulff, 1969). In more populated areas, domestic pets might similarly act as carriers of individuals; in Barkley Sound, the broken shoreline and isolation of these particular field sites reduces the influence of humans or domestic pets, but the general ease of shoreline access to splashpools does not preclude this kind of disturbance in other areas. The viability and effective distance of dispersal by these terrestrial agents would seem to be limited by: 1) restriction of dispersal routes for land mammals on island sites; and 2) the movement of these animals inland and through forests to a much greater extent than along exposed rocky shores. As mentioned above,

Long-Distance Biotic Agents

Avian Carriers: As anticipated, the handling and preparation of the bird specimens precluded reliable determination of the number of individuals, and which life-history stages, might potentially have been carried by the birds. Although the museum specimens I have examined to date have carried no *T. californicus* in their plumage, species endemic to the study area (from Campbell et al., 1990) have been observed to retain other microcrustacea, including copepods and isopods. Harpacticoid copepods

typically represent the second-most abundant fauna in meiobenthic communities[3], and as such are probably good candidates for incidental collection in the plumage or on the appendages of foraging birds. For other Crustacea, Schmitt (1967, p.100) provides anecdotal accounts of gulls and penguins foraging selectively for amphipods. Moreover, the coastal area extending through Barkley Sound from Baja, California, to the Arctic is a major migratory corridor for dozens of bird species endemic to the Barkley Sound area, with some of these (e.g., red knot, *Calidrus canutus*) extending their range to western Europe (Campbell et al., 1990) or the Atlantic coast of North America (where *T. californicus* has not been described).

Assuming a 10 - 15% recovery of desiccated individuals and a founding copepod population of eight to 10 individuals (see Chapter 3), only 100 to 150 *T. californicus* retained by a bird (or birds) foraging in the supralittoral zone would be sufficient to provide dispersal in this manner. At the *in situ* population densities *T. californicus* may attain (often in excess of 20 individuals $\cdot L^{-1}$, with a mean in excess of 750 individuals $\cdot L^{-1}$ over much of the year, Chapter 5), such estimates are not unreasonable and provide an avenue worth further examination. Clearly, examination of a larger number of bird specimens, captured by happenstance or with a banding permit in the vicinity of the field sites, is required to evaluate more accurately the potential of birds as dispersal agents of *T. californicus.*

Rafting: Transport of copepods on driftwood or broken macroalgae also provides a plausible mechanism for dispersal (P. K. Dayton, pers. comm.). *T. californicus* pools often contain wave-swept debris, and were this material "colonized" by copepods, its subsequent redistribution might carry some individuals along the shore. Given the high elevation of most of the pools in Barkley Sound, the provision and relocation of raft material would be accompanied by intense wave action, and it would

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[3] Second only to nematodes in terms of absolute abundance (Hicks and Coull, 1983).

be difficult – if not impossible – to determine the proportion of copepods transported by rafts, relative to those carried by the waves themselves.

CONCLUSIONS

Splashpool colonization by *T. californicus* appears to occur irrespective of vegetation by macroflora, suggesting that *in situ* the copepod is most likely a bacteriovore or rasps a mixed diet of available food resources off the substratum. The extreme flux in physical conditions experienced in supralittoral pools may create an ephemeral habitat for *T. californicus*, but one which restricts the presence of potential predators or competitors over much of the year. Analyses and discussion of *T. californicus*' population response to the conditions within this extremely stressful habitat will be the subject of the following chapters.

Redistribution by wave splash may partially explain the position of *T. californicus* pools relative to average water levels, but the heterogeneity of adjacent metapopulations and the conspicuous absence of the copepod on sandy beaches or in offshore areas does not support longshore transport as an agent of dispersal. Responses of *T. californicus* to chemical secretions or sudden disturbances within this refuge are likely more effective at retaining position than assisting dispersal, but probably function primarily under tranquil conditions.

Transport by other invertebrates or incidental mammals may occur over short distances, but may also make the copepod more susceptible to predation via its association with a larger organism. Land mammals may redistribute copepods among supralittoral water deposits, but this does not explain the degree of island colonization observed. Maritime birds may therefore be the only effective dispersal agents over any appreciable distance.

CHAPTER 2: THE RESPONSE OF *TIGRIOPUS CALIFORNICUS* TO CHLOROPHYTIC MACROALGAE, INCLUDING *CLADOPHORA TRICHOTOMA* KÜTZING

INTRODUCTION

"There is no banquet but some dislike something in it."

— THOMAS FULLER (1732)

Tide pool classification, algal surveys, community dynamics and succession in the littoral zone have been addressed by a legion of studies, including Fraser (1936a); Kain (1958); Gustavsson (1972); Dethier (1982) and those reviewed in Metaxas and Scheibling (1993). Among these, the supralittoral zone provides a unique intermediary between intertidal habitats and emergent substrata. Pools located above mean high water (MHW) may be more directly influenced by atmospheric conditions than tidal action (Igarashi, 1959; Egloff, 1966; Vittor, 1971; Morris and Taylor, 1983), and commonly experience extreme fluctuations in various water properties, including: temperature (due to sunlight absorption and lithic heat retention), salinity (due to runoff, precipitation, freezing or evaporation), oxygen and pH (due to biological activity).

Common to the fringes of temperate supralittoral pools is the alga *Cladophora trichotoma* (C. Agardh) Kützing (common name = "green ball"). Befitting its name, *C. trichotoma* grows in hemispherical, bright green tufts 3 to 6 cm in diameter and is composed of short, branched filaments up to 1.0 mm in length and 0.2 mm in diameter (Scagel, 1957; Waaland, 1977). Representatives of this complex and ill-defined genus are found on sand and mud flats (Guberlet, 1956) as well as high on exposed rocky shores and reefs (Waaland, 1977) from British Columbia to Mexico. The opportunistic chlorophyte grows very rapidly in thick, turf-like mats - to the extent that it potentially

competes with sessile invertebrates for attachment space - until it is sloughed off by wave action.

Equally common to the exposed, rocky Pacific coastlines of North America is the harpacticoid copepod *Tigriopus californicus* (Baker). The species has been described in high elevation supralittoral splashpools from Alaska to Baja, California (Monk, 1941; Belser, 1959; Dethier, 1980) and similar habitats have been reported for its congeners, including *T. brevicornis* (Harris, 1973, in the U.K.), *T. fulvus* (Battaglia et al., 1978, in Italy), and *T. japonicus* (Takano, 1971, in Japan). Faced with the characteristics of its ephemeral and often barren supralittoral habitat, it is not surprising that the genus demonstrates a remarkable tolerance to physical conditions, including sudden or extreme changes in temperature and salinity (Ranade, 1957; Huizinga, 1971; Kontogiannis, 1973).

Over nearly two years, seasonal changes in supralittoral macroalgal composition and *Tigriopus californicus* distribution and abundance were monitored in Barkley Sound, British Columbia. Throughout the year, *T. californicus* populations are commonly found in pools containing algal crusts, green algae such as *Enteromorpha compressa* (Linnaeus) Greville and *E. intestinalis* (Linnaeus) Link, as well as in pools lacking any upright vegetation. However, pools containing *Cladophora trichotoma* are not observed to retain populations of *T. californicus*. During preliminary studies, even *C. trichotoma* pools inoculated with *T. californicus* cultures showed no evidence of copepod habitation after only a few days. Among the agents potentially responsible for this apparent exclusion are: 1) more direct exposure to wave action (Igarashi, 1959); 2) atmospheric conditions and water properties (Vittor, 1971; Morris and Taylor, 1983); 3) nutrient supply ; 4) co-incident fauna (Dethier, 1980); and 5) macromolar compounds such as chemical attractants or anti-feedants (Bozic, 1975; Shaw, 1994).

Tigriopus species have been experimentally associated with chemically-mediated behavior for at least two decades, albeit mainly from behavioral inference and without the identification or isolation of the agent(s) involved. Bozic (1975) proposed an

'aggregation pheromone' response in *Tigriopus* (I assume *fulvus*) to vessels which previously held copepod cultures. Studies by Kahan et al. (1988), Lazzaretto et al. (1990), Kahan (1992), and Lazzaretto and Salvato (1992) also described density-dependent chemical messengers which may variously regulate maternal and cannibalistic behaviors in *T. californicus, T. fulvus* and *T. japonicus.* Yet, while chemically-mediated behavior or population response to noxious substances can be readily observed, the isolation and identification of these chemical exudates is a formidable undertaking even under laboratory conditions. The elucidation of recognition factors and their potential to elicit response(s) is more difficult still. Recognition factors doubtless play instrumental but differing roles in free-flowing, intermittently-mixed, or isolated aquatic systems. Any of these conditions may exist in temporary rock pools or supralittoral splashpools, complicating both the activity and detection of chemical agents. In a small, isolated water deposit, one can speculate only that the combined influence of an organism's own secretions, the chemical attractants and anti-feedants released by its food resources and the compounds released from prospective predators must create a tantalizing (if confusing) aromatic cocktail.

The current chapter provides data examining the validity and extent of the apparent exclusion of *Tigriopus californicus* from pools containing *Cladophora trichotoma.* In doing so, the possible influence of chemical exudates may be revealed by regulating or isolating more obvious parameters affecting splashpool communities, including the relative degree of wave splash, pool volume, temperature, salinity, and substrate type. For the current chapter, the alga *Enteromorpha compressa* and its conspecific *E. intestinalis* will provide phycological comparison with another chlorophyte. Although the phaeophyte *Scytosiphon lomentaria* is also commonly found in winter pools containing *T. californicus* (Chapter 1), and possesses long, grass-like filaments akin to *Enteromorpha*, during the summer *S. lomentaria* occurs in its alternate phase, the encrusting *Ralfsia pacifica*. This marked difference in algal morphology

between seasons was the predominate reason for not also including a similar comparison of "substrate type" between *C. trichotoma* and *S. lomentaria.*

MATERIALS AND METHODS

Field sites: Splashpools on Wizard Islet (Lat. 48°52'N: Long. 125°10'W) and Helby Island (48°51'N: 125°10.5'W) in southeastern Barkley Sound were surveyed during intervals in January, May, and August, 1995 (see Figure 1.1). Each pool was mapped according to the methods described in Chapter 1, while copepods were sampled by dividing the surface of each pool into a numerically-assigned sextet, then rolling a die to select the position of three random samples taken by a 30 mL graduated pipette drawn along the substratum (also detailed in Chapter 1).

On each island, all pools selected for study were located within 100 m of each other, and were sampled within hours on the same day, hence atmospheric conditions were assumed constant for each sampling day. While not measured directly, the possible effects of exposure to wind or wave action were isolated by assigning treatments within each area by stratified random sampling according to shoreline elevation (greater than 3.0 m = "high elevation"; less than 3.0 m = "low elevation") and orientation according to leeward (= "low exposure") or windward (= "high exposure") position on a given outcrop. Pools were additionally classified as having either: 1) no visible vegetation; 2) growth of *Enteromorpha compressa* or a combination of *E. compressa* + *E. intestinalis* to the extent of at least 30% cover; or 3) growth of *Cladophora trichotoma* to the extent of at least 30% cover. The 30% level was arbitrarily chosen as an amount of algal growth that could significantly affect: 1) the degree of protection afforded *T. californicus* against desiccation, wave splash, or predation; 2) water conditions *in situ*, including oxygenation, pH, and dissolved organic material; and 3) the amount or concentration of exudates potentially produced.

Field Measurements: Splashpool pH was recorded using a Fisher Alkacid full-range pH kit; salinity using a Hanna Model 9033 multi-range conductivity meter; oxygen using a YSI Model 57 oxygen meter (calibrated for salinity from 0 to 40‰[1]); and temperature using a Fisher field-protected thermometer. Temperatures were recorded at each 5 cm depth (when permitted by pool depth) to determine the degree of thermal stratification.

Differences in *Cladophora*, *Enteromorpha*, and non-vegetated pool parameters including surface area, volume, temperature, salinity, percent-cover of macroalgae, and faunal abundance were evaluated using a single-factor Kruskal-Wallis analysis of variance by ranks or Mann-Whitney test at $\alpha = 0.05$ (Zar, 1984). For those pools containing *T. californicus*, samples were collected in triplicate on each day of the sampling interval (5 days) and returned to the laboratory for identification and enumeration. Pools lacking *T. californicus* were inoculated with approximately equal numbers of individuals (100 - 300 individuals $\cdot L^{-1}$ pool volume, transferred from inhabited pools) and sampled each day over the same interval. None of the treatment pools was stringently scoured of all copepods prior to inoculation (*sensu* Coull and Wells, 1983), and it is possible that some pools surveyed and determined to 'lack copepods' may have contained small resident populations which were later sampled. Scouring, pumping, or other means of treatment preparation were avoided as this may have produced undesirable side effects, particularly with regard to any chemical exudates in the resident pool water.

Laboratory Cultures: Samples of *E. compressa* and *C. trichotoma* for laboratory use were collected from each site and maintained in a flow-through sea water table at *ca.* 15°C, 5 to 8 mg $\cdot L^{-1}$ oxygen and 30 to 35‰ salinity. *Tigriopus californicus* were collected and retained in 2 L Erlenmeyer flasks at room temperature. From these cultures, egg sacs were removed from gravid females and allowed to hatch, providing a culture of nauplii for use in microcosms. To correct for acclimation effects (i.e., previous

[1] Oxygen data was therefore not recorded for pools with salinity greater than 40‰.

exposure to bacteria, macroalgae, chemical agents), copepod cultures from all pool types were combined, then gradually converted to prepared seawater *sensu* Morel at al. (1979) over three to four days.

Laboratory Microcosms: In order to better control external influences and provide greater resolution of *T. californicus* response to the presence of *E. compressa* and *C. trichotoma* in stagnant solution, the following microcosms were prepared: Plastic 1 L Nalgene bottles were cut width-wise into 500 mL 'bowls' that were then filled with *ca.* 400 mL of unfiltered sea water and *ca.* 15 g (wet weight) of either *E. compressa* + *intestinalis* or *C. trichotoma.* The algae were rinsed in sea water and wiped dry using paper towels, but no other attempt was made to remove any organisms living on or among the algal filaments. A total of 18 microcosms (6 x each treatment type) were prepared for immature copepods (eggs and hatched nauplii - stages N-I to N-VI), and a second set of 18 treatments for juvenile (copepodite stages C-I to C-III) and adult (stages C-IV to C-VI) using the cultures described above. The microcosms were retained at room temperature and observed for five days or until the copepods showed no further decline in numbers (death or apparent death of individuals).

RESULTS

Pool Conditions: Although isolated splashpools were observed to experience substantial changes in surface area or volumetric flux due to evaporation or precipitation, different types of pools (i.e., pools without macroalgae, those containing *C. trichotoma*, or those containing *E. compressa*, Table 2.1) did not differ statistically in pool dimensions or changes in water volume (Kruskal-Wallace $H_{0.05,6,6,6}$, $0.05 < P < 0.1$) for any of the treatment types. While surface area and pool volume each exhibited a tremendous range of values within treatment type, the decline in *T. californicus* numbers was similar, as indicated by the mean ± 1 standard error values, even between pools of high and low exposure to direct wave action. Weather was unseasonably warm, dry, and stable during

the spring (May, 1994) interval, surpassing even the August climatic conditions for atmospheric temperature, hours of sunlight and overall rate of pool evaporation.

Measured pH was not statistically different between *Enteromorpha, Cladophora,* or non-vegetated pools at any time, and usually varied between 6.0 and 8.0, with occasional instances of up to 10.0 in August. In spring and summer, pools containing *C. trichotoma* had significantly higher oxygen readings ($H_{0.05,6,6,6}$ =7.9565, $0.01 < P < 0.02$) than *E. compressa* or barren pools, likely the result of enhanced photosynthetic activity. Although salinity was noted to be highly variable within and among pools, the range of values measured (mean ± S.E.) did not differ significantly (Mann-Whitney $U_{0.05(2)6,6}$= 30, $0.05 < P < 0.1$) among treatment types within any of the seasons. Similarly, water temperature was noted to vary only slightly within a single pool or among pools, and would vary approximately with atmospheric conditions. None of the pools was distinct in this variable (i.e., beyond the normal range of values found among all pools), and variation among pools during any given sampling day was rarely more than 2 - 3 °C. Expectedly, water temperature during the winter (January) sampling period was significantly lower than during either the spring or summer intervals. A summary of these conditions is provided in Table 2.1.

Abundances of *Enteromorpha compressa, E. intestinalis* and *Cladophora trichotoma* were generally lower in January, when various encrusting species were more apparent. While abundance of *E. compressa* rarely exceeded 30% coverage of the substratum in pools with or without *T. californicus,* the percent-cover of *C. trichotoma* was generally higher, averaging 42.1 ± 16.4% (all pools) in August.

In January, *T. californicus* population numbers were lowest in all treatment types (142.4 ± 183.2 individuals · L^{-1}) and disparity in copepod abundance among pools with versus without *C. trichotoma* is less evident in January than in either the May or August results. Overall percent-cover of *C. trichotoma* was also lowest in January (15.8 ± 10.8% compared to 35.0 ± 25.5% in May and 42.1 ± 16.4% in August). Absolute percent-cover

TABLE 2.1. Summary of *in situ* conditions for pools containing *T. californicus* in Barkley Sound. Treatments (same-substrate pools) differing significantly from one another between sampling intervals indicated by [‡]; Values differing significantly from other treatment types during the same sampling interval indicated by [†] (Kruskal-Wallace H at $P < 0.05$). Values presented as mean ± S.E.

Treatments containing *Enteromorpha compressa + E. intestinalis*

PARAMETER		JANUARY, 1995 SAMPLING	MAY, 1995 SAMPLING	AUGUST, 1995 SAMPLING
No. pools sampled		19	19	10
Avg. Air Temp. (°C)	[‡]	5.5 ± 5.2	17.2 ± 6.1	15.5 ± 7.3
(range)		(-4 - 10)	(8 - 21)	(10 - 25)
Avg. Elevation (m)		3.8 ± 1.0	3.9 ± 0.7	3.8 ± 0.7
(range)		(2.5 - 6.7)	(2.8 - 5.0)	(2.8 - 5.0)
Avg. Volume (m^3)		0.9 ± 1.61	0.3 ± 0.44	0.3 ± 1.83
range		(0.2 - 5.0)	(0.01 - 0.40)	(0.03 - 3.66)
Avg. pH		7.4 ± 0.7	8.4 ± 0.7	7.8 ± 1.2
(range)		(6.2 - 8.3)	(7.1 - 9.5)	(6.8 - 10.0)
Avg. Oxygen (mg/L)		6.1 ± 1.4	5.7 ± 3.3	5.6 ± 2.11
(range)		(3.5 - 7.8)	(1.1 - 9.0)	(1.6 - 8.3)
Avg. Pool Temp (°C)	[‡]	9.7 ± 0.8	20.4 ± 4.2	25.0 ± 3.4
(range)		(9 - 12)	(10 - 25)	(20 - 32)
Avg. Salinity (‰)		17.9 ± 8.5	52.2 ± 31.4	32.7 ± 14.6
(range)		(5.4 - 30.9)	(18.2 - 109)	(20 - 62.3)
%-Cover of *Enteromorpha*		16.7 ± 13.6	28.9 ± 28.6	19.0 ± 24.6
(range)		(5 - 50)	(5 - 90)	(5 - 17)
T. californicus/L**		349 ± 705	1870 ± 1567	1175 ± 578
(range)		(33 - 2440)	(600 - 6800)	(650 - 2000)

(continued)

** Individuals per liter of pool volume, inclusive of all life-history stages.

TABLE 2.1. (continued)

Treatments containing *Cladophora trichotoma*

PARAMETER		JANUARY, 1995 SAMPLING	MAY, 1995 SAMPLING	AUGUST, 1995 SAMPLING
No. pools sampled		12	18	12
Avg. Air Temp. (°C)	[‡]	5.5 ± 5.2	17.2 ± 6.1	15.5 ± 7.3
(range)		(-4 - 10)	(8 - 21)	(10 - 25)
Avg. Elevation (m)		3.6 ± 0.7	3.7 ± 1.2	3.6 ± 0.6
(range)		(2.6 - 5.0)	(2.8 - 6.7)	(2.5 - 4.5)
Avg. Volume (m^3)		1.3 ± 2.06	0.3 ± 0.44	0.5 ± 0.80
range		(0.08 - 5.46)	(0.01 - 1.49)	(0.02 - 2.88)
Avg. pH		7.1 ± 0.3	7.5 ± 0.4	7.4 ± 0.9
(range)		(6.5 - 7.6)	(7.0 - 8.1)	(6.0 - 9.1)
Avg. Oxygen (mg/L)		7.9 ± 1.1	11.0 ± 2.6	8.9 ± 0.7
(range)		(7.0 - 10.1)	(7.0 - 13.2)	(8.5 - 10.7)
Avg. Pool Temp (°C)	[‡]	9.8 ± 1.3	21.3 ± 2.1	22.6 ± 2.8
(range)		(8 - 12)	(16 - 25)	(19 - 27)
Avg. Salinity (‰)		27.3 ± 3.9	35.1 ± 10.1	35.5 ± 6.7
(range)		(16.9 - 31.1)	(29.4 - 74.1)	(29 - 52.8)
%-Cover of *Cladophora*		15.8 ± 10.8	35.0 ± 25.5	42.1 ± 16.4
(range)		(5 - 40)	(5 - 80)	(20 - 70)
T. californicus/L **		84 ± 112	35 ± 103	0
(range)		(0 - 175)	(0 - 333)	(0 - 0)

(continued)

** Individuals per liter of pool volume, inclusive of all life-history stages.

TABLE 2.1. (continued)

Treatments without macroalgae.

PARAMETER		JANUARY, 1995 SAMPLING	MAY, 1995 SAMPLING	AUGUST, 1995 SAMPLING
No. pools sampled		11	16	17
Avg. Air Temp. (°C)	[‡]	5.5 ± 5.2	17.2 ± 6.1	15.5 ± 7.3
(range)		(-4 - 10)	(8 - 21)	(10 - 25)
Avg. Elevation (m)		3.9 ± 1.4	4.2 ± 1.0	3.8 ± 1.0
(range)		(1.5 - 6.7)	(2.6 - 6.0)	(2.6 - 6.7)
Avg. Volume (m^3)		0.72 ± 1.68	0.5 ± 1.12	0.8 ± 0.99
range		(0.01 - 5.4)	(0.1 - 3.91)	(0.04 - 2.64)
Avg. pH		7.3 ± 0.5	7.0 ± 0.7	7.2 ± 0.7
(range)		(6.5 - 8.1)	(6.0 - 8.0)	(6.2 - 8.5)
Avg. Oxygen (mg/L)		6.5 ± 1.6	7.5 ± 0.9	4.1 ± 2.1
(range)		(4.5 - 8.0)	(6.2 - 8.6)	(1.7 - 7.2)
Avg. Pool Temp (°C)	[‡]	9.7 ± 1.6	21.5 ± 1.9	25.4 ± 2.7
(range)		(7 - 12)	(18 - 25)	(20 - 29)
Avg. Salinity (‰)		25.1 ± 6.5	51.0 ± 34.6	39.5 ± 13.6
(range)		(9.2 - 30.7)	(6.1 - 125)	(29.9 - 89.2)
%-Cover of Algae	[†]	0	8.8 ± 16.2 *	0.6 ± 2.4*
(range)		(0 - 0)	(0 - 60)	(0 -10)
T. californicus/L **		78 ± 124	1742 ± 2002	534 ± 342
(range)		(0 - 344)	(133 - 8229)	(0 - 1800)

* Includes encrusting algal species not identified in the context of this study.
** Individuals per liter of pool volume, inclusive of all life-history stages.

did not differ with season for either *C. trichotoma* or *E. compressa*, and an inverse correlation is evident only between *C. trichotoma* and *T. californicus* abundance (Pearson's coefficient = -0.986, $P < 0.05$ over all seasons).

Despite the apparent similarity between the chemical, physical and phycological features of the pools, only those pools containing *C. trichotoma* retained lower abundances of *T. californicus*, regardless of life-history stage and particularly in May and August (mean 35 ± 103 and 84 ± 112 individuals · L^{-1}, respectively, from Table 2.1). Mean values rounded to the nearest whole individual). Pools containing *C. trichotoma* during May sampling also showed a higher density of littorines (*Littorina* spp., at 10 ± 2.3 10 cm^{-2}) than either *E. compressa* pools or barren pools (4 ± 3.5 10 cm^{-2} and 2 ± 5.4 10 cm^{-2}, respectively; Mann-Whitney U values significant at $0.02 < P < 0.05$). Larger, vegetated pools more frequently contained gammariid amphipods and isopods, however the occurrence of other invertebrates (shore crabs, limpets, *Chthamalus* and *Balanus* barnacles) or incidental vertebrates (mink, deer, shore birds) was too infrequent in the field sites to derive any reliable statistical analyses.

Field Results: Expectedly, copepod abundance was found to be extremely 'patchy,' with high variances confounding analyses for statistical difference between treatments (Table 2.1). The response of copepod populations following inoculation of splashpools of all treatment types is summarized in Figure 2.1, and by life-history stage in *C. trichotoma* pools in Figure 2.2. Juvenile and adult copepodite stages (C-I to C-VI) demonstrated the greatest decline in overall number, while nauplius response (stages N-I to N-VI) was highly variable but consistent regardless of pool type. Whether this was due to actual numbers or sampling error cannot be determined due to the difficulty of collecting, handling and identifying the nauplii *in situ*.

Laboratory Results: Results from the laboratory microcosms are summarized in Table 2.2 and Figure 2.3. After five days of observation, the microcosms containing *C. trichotoma* retained fewer (18.6 ± 7.3 %-survival) copepodites and adult *T.*

californicus (stages C-I to C-VI) than other treatments ($H_{0.05,6,6,6}$= 8.34; 0.005 < P < 0.01). In microcosms inoculated with nauplii only (stages N-I to N-VI), no statistical difference was noted between treatments. After five days, the more advanced nauplii began molting to copepodites and were transferred to a separate culture where they appeared to mature normally.

Figure 2.3 summarizes the average response of *T. californicus* to the presence of *C. trichotoma* in the six laboratory microcosms. Here, the effects of wind, precipitation, and wave splash are removed, and under-sampling of any life stages is unlikely, given the smaller, controlled volume. (Error may be introduced, however, as individuals are damaged or lost with the repeated transfer of solution for observation purposes.) Once again, the most significant deleterious effects can be seen among adult (stages C-IV to C-VI) *T. californicus*, including the complete mortality of all gravid females in the microcosms. While the net decrease in population is similar to that noted in the field treatments, the most substantive decline in microcosm *T. californicus* was not noted until Day 3-4, compared to Day 0-1 in field treatments. As with the field sites, the overall number of nauplii in the microcosms, somewhat variable in initial abundance, remained at essentially similar levels throughout the period of observation.

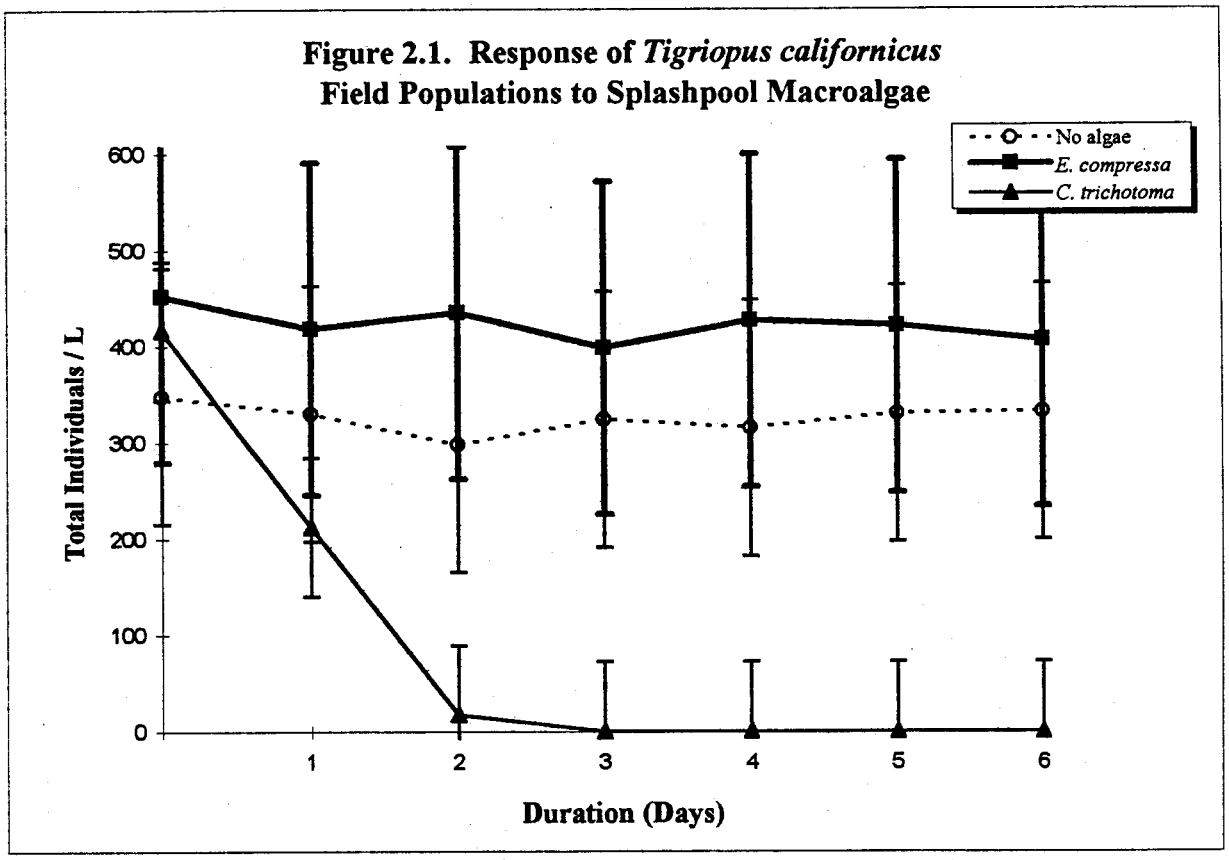

FIGURE 2.1. Response of *Tigriopus californicus* field populations to the presence of splashpool algae. Treatments contained either *Enteromorpha compressa+ intestinalis, Cladophora trichotoma*, or no algal material. Results are the average of 6 pools of each substrate type following inoculation of *T. californicus* in May and August, 1995. As a plot of averaged results, error bars represent standard error of the mean (S.E.).

TABLE 2.2. Five-day population response of *T. californicus* in microcosms containing *E. compressa, C. trichotoma* or lacking algal material. Significantly lower survivorship by treatment type indicated by [†] (Kruskal-Wallace H at $P < 0.05$). Values presented as mean ± S.E.

Microcosms containing *Enteromorpha compressa + intestinalis.*

Microcosm count (Avg. of 6 treatments)	***T. californicus* nauplii (stages N-I to N-VI)**	***T. californicus* copepodites+adults (stages C-I to C-VI)**
Initial count (individuals/L)	78 ± 9.4	162 ± 8.9
Count after 5 days	71	152
net gain/(loss)	(7 ± 2.2)	(10 ± 1.1)
% gain /(loss)	(9.0 ± 2.2)	(6.2 ± 1.1)
% survival	91.0 ± 3.8	93.8 ± 5.4

Microcosms containing *Cladophora trichotoma.*

Microcosm count (Avg. of 6 treatments)	***T. californicus* nauplii (stages N-I to N-VI)**	***T. californicus* copepodites+adults (stages C-I to C-VI)**
Initial count (individuals/L)	50 ± 4.6	140 ± 6.1
Count after 5 days	41	[†] 26
net gain/(loss)	(9 ± 5.3)	(114 ± 9.2)
% gain /(loss)	(18.0 ± 5.3)	(81.4 ± 9.2)
% survival	82.0 ± 6.2	[†] 18.6 ± 7.3

Microcosms without macroalgae.

Microcosm count (Avg. of 6 treatments)	***T. californicus* nauplii (stages N-I to N-VI)**	***T. californicus* copepodites+adults (stages C-I to C-VI)**
Initial count (individuals/L)	42 ± 3.9	178 ± 9.2
Count after 5 days	35	180
net gain/(loss)	(7 ± 6.3)	2 ± 1.0
% gain /(loss)	(16.7 ± 6.3)	1.1 ± 1.0
% survival	87.2 ± 0.03	95.6 ± 0.1

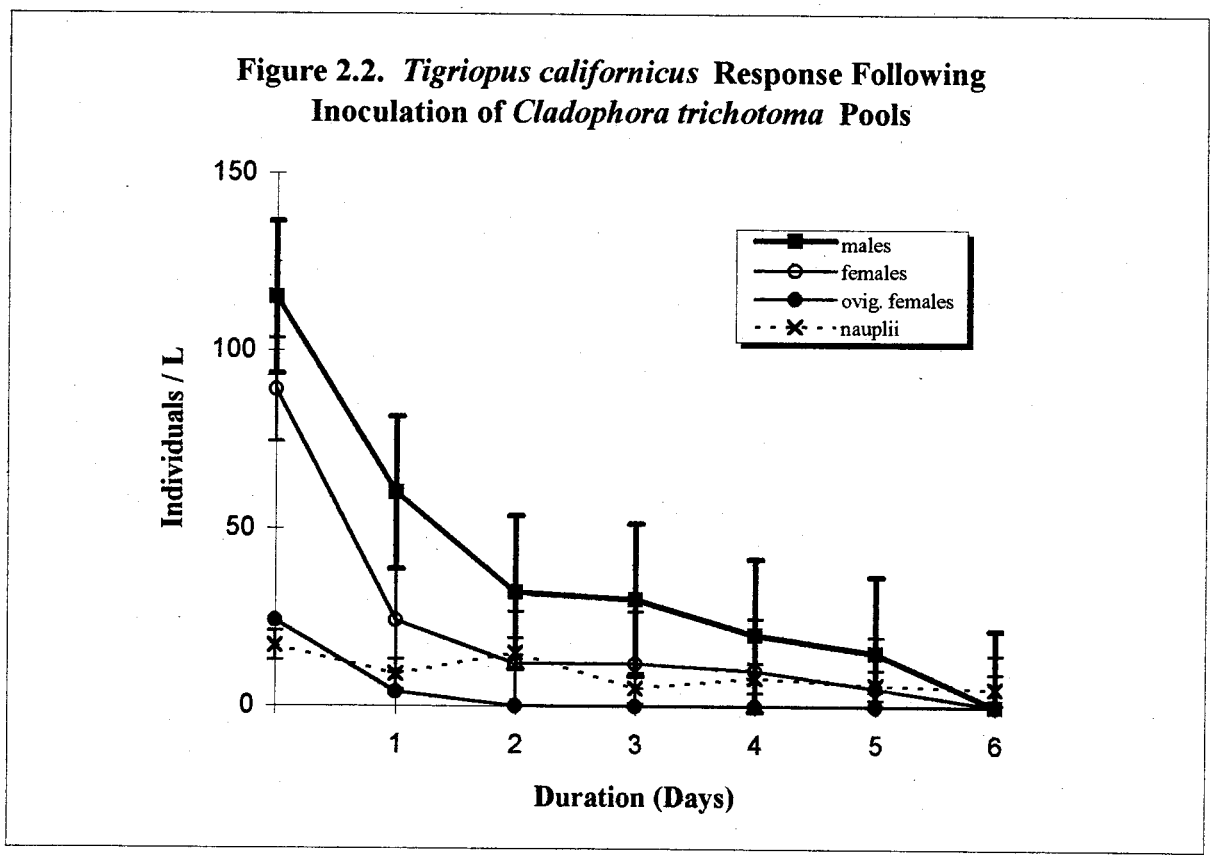

FIGURE 2.2. *Tigriopus californicus* response following inoculation of *Cladophora trichotoma* pools. As plotted, 'nauplii' = stages N-I to N-VI; 'male' and 'female' = stages C-I to C-VI, where gender could be established. As a plot of averaged results, error bars represent standard error of the mean (S.E.).

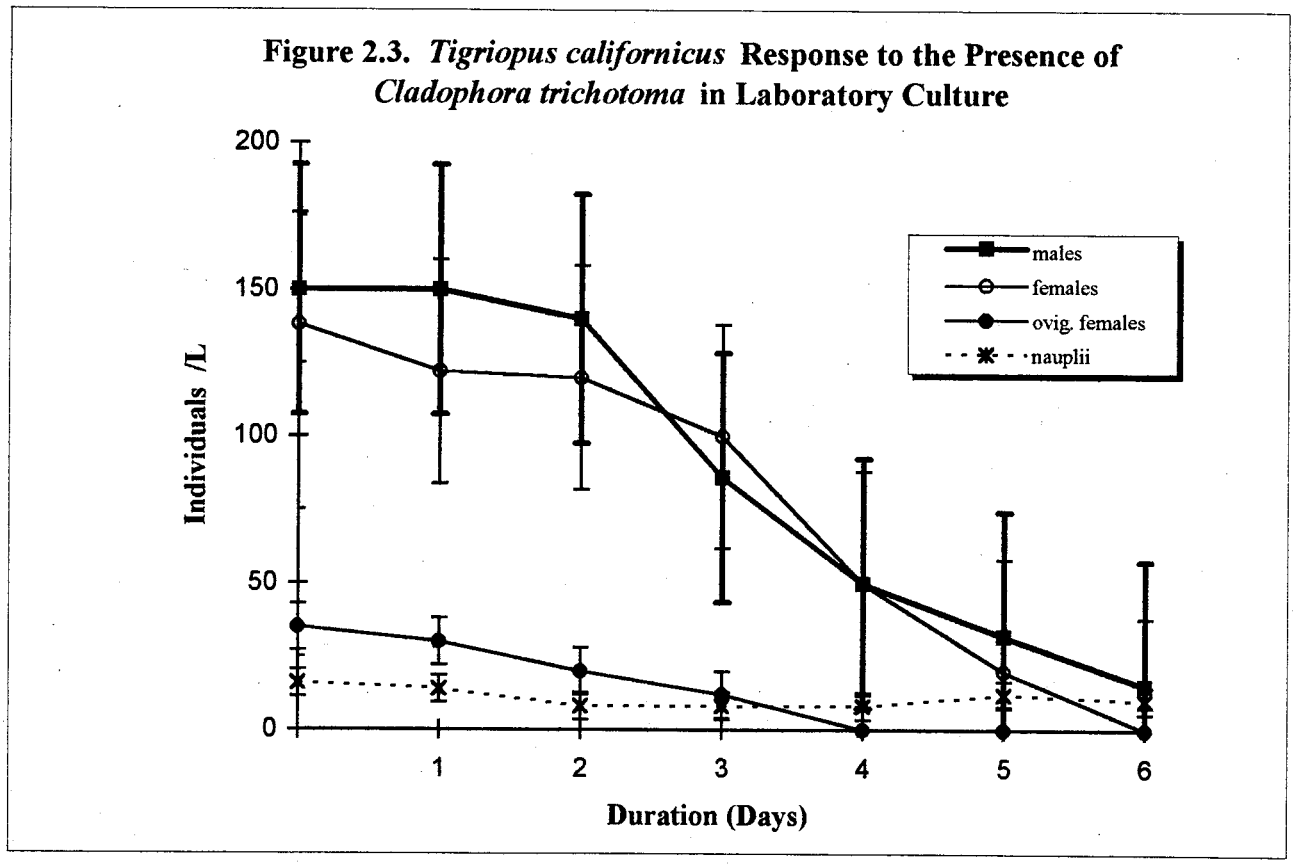

FIGURE 2.3. *Tigriopus californicus* response to the presence of *Cladophora trichotoma* in laboratory microcosms. Note that while the net response is similar to that observed *in situ* (Figure 2.2), the most rapid decline in abundance occurs later following inoculation. As plotted, 'nauplii' = stages N-I to N-VI; 'male' and 'female' = stages C-I to C-VI, where gender could be determined. As a plot of averaged results for 6 x 500 mL, error bars represent standard error of the mean (S.E.).

DISCUSSION

On first consideration, the co-occurrence of *Tigriopus californicus* with dense growths of supralittoral macroalgae would seem an ideal mutualism: The copepods would receive protection from exposure and predation, oxygen from photosynthesis, and a supply of dissolved organic matter and bacteria associated with the alga's surface. In exchange, the algae receive the benefit of nitrogen excreted from the copepods, principally in the form of ammonia (89.7% of the total nitrogen excreted and estimated at 27.2 μg N· mg dry $wt^{-1} \cdot day^{-1}$ at 15°C for adult female *T. brevicornis,* per Harris, 1973). As mentioned above, several factors must be considered in attempting to resolve why *T. californicus* does not appear to co-occur with *C. trichotoma*, including: 1) unique water conditions in pools containing *C. trichotoma*; 2) comparative degree of pool exposure to waves; 3) coincident fauna, particularly potential predators of either nauplii or juvenile (copepodite) life-history stages; 4) food supply; and 5) the survival and persistence of larval life-history stages.

Water Conditions: The range and variation of water properties measured in this study are comparable to previously-published values for supralittoral pools (Morris and Taylor, 1983; examples in Metaxas and Scheibling, 1993). Pools containing *C. trichotoma* demonstrated no unique properties other than oxygen partial pressure (though admittedly, parameters more indicative of water condition such as levels of nitrate, phosphate, microflora or phytobenthos were not included in the current analysis). That enhanced oxygen content alone is somehow toxic to *T. californicus* is unlikely, given the relatively large surface area of the splashpools (4.8 ± 10.9 m^2 over an average depth of 7 ± 3.2 cm). The values of 1.2 to 13 mg $\cdot L^{-1}$ oxygen recorded here compare to "non-lethal" oxygen levels reported by Kontogiannis and Barnett (1973), whose results suggest instead that *T. californicus* can be impaired by a reduction in oxygen partial

pressure (as by obstruction of the pool surface/atmosphere interface), an effect that might be even more significant at high population densities.

Comparative Exposure: Although the intertidal distribution of *Enteromorpha, Cladophora* and *Tigriopus* may overlap (Fraser, 1936a; Gustavsson, 1972; Dethier, 1980), *Cladophora* is generally found lower on the shore (Guberlet, 1956; Scagel, 1957; Waaland, 1977). The relatively greater exposure of the lower *C. trichotoma* pools to wave splash may in part explain the absence of copepods from these pools, which concurs with published observations including Igarashi (1959), Vittor (1971), and Dethier (1980). Igarashi (1959) noted an inverse correlation between the age and stability of *Tigriopus* (I assume *japonicus*) populations and the frequency of wave wash. *Tigriopus* copepods are not noted to be strong swimmers (e.g., Fraser, 1936a, and pers obs.), are an attractive prey item to fish and invertebrate predators (Dethier, 1980) and as a result may not remain long in the water column.

Although wave exposure was not measured directly in the current study, among pools 1) within a few meters of each other; 2) at the same elevation; and 3) differing visibly only in the type of vegetation, only those pools containing *C. trichotoma* retained significantly fewer copepods. A similar trend was also observed among pools of greater or lesser elevation and/or exposure to wave action, but whether the loss of copepods from those pools was alternately due to hydrodynamic consequences, surficial features, or finer-scale differences in wave activity is not clear. From observations of culture organisms (Chapter 4), *T. californicus* does not exhibit self-directed swimming until the N-III stage (diameter 100 - 200 μm), and may therefore be more susceptible to other influences, such as wash-out by waves, cannibalism, or predation during the first few days after hatching.

Although *T. californicus* populations also declined in the presence of *Cladophora* in laboratory microcosms, the effect was delayed (to Day 3-4) over that noted in field treatments (Day 0-1). The decline in the number of copepods (especially adults) in the

absence of wave splash or atmospheric effects suggests the action of a secondary deleterious agent on these life-history stages. The overall decline in copepod populations introduced to *Cladophora* pools *in situ* is likely due to the additional influences of: 1) under-sampling of copepods from the larger, irregular volume; 2) relatively greater wave action on the generally lower *C. trichotoma* pools; and 3) the transport of adult *T. californicus* out of *C. trichotoma* pools either passively by wave wash, or actively by swimming or crawling. Egloff (1966) also proposed 'hitch-hiking' on the carapaces of grapsid or pagurid crabs as a means of *T. californicus* transport between pools, a suggestion reiterated by Dethier (1980) and Burton and Feldman (1981), but see Chapter 1.

Coincident Fauna: The significantly greater number of littorines in *C. trichotoma* pools may provide either competition to or predation on *T. californicus* populations. It is not known whether littorines or barnacles cull *Tigriopus* populations by grazing nauplii from the bottom of the pools or filtering them from the water column. Though present in much smaller numbers, amphipods may also consume *T. californicus*, however pools are routinely found with thriving copepod populations despite the additional presence of amphipods, isopods and even sculpins, particularly during the summer months (Chapter 1). Littorines are also commonly found with *T. californicus* in non-vegetated and comparatively sheltered *Enteromorpha* pools, though in lesser numbers. Given the remarkable densities at which *T. californicus* may be found (up to 200,000 L^{-1}, from Chapter 3), it is unlikely that other meiofauna are out-competing *T. californicus* for some common food resource. That littorines are responsible for producing the substance apparently noxious to copepods is not supported by the laboratory results, where snails were excluded from all microcosms yet the *T. californicus* populations declined.

Nutrient Supply: The macroalgae present are probably inconsequential as a food resource for *T. californicus*. An examination of the gnathobase and mandibles (see Egloff, 1966, p. 11) suggests that *T. californicus* is not an herbivore or filter-feeder, but

most closely approximates the 'prey-crusher' variety described by Marcotte (1977) and discussed in Hicks and Coull (1983). Given this, *T. californicus* most likely browses any available surface, feeding on a mixture of benthic diatoms and bacteria (*cf.* Provasoli et al., 1959, for laboratory culture). Any substrate which encourages the growth of benthic microflora by: 1) the accumulation of organic debris; 2) enhancing the available surface area, or 3) having lesser accumulations of sedimentary material would therefore suit *T. californicus* for the provision of food. This suggestion is particularly relevant when one considers the diversity of 'food' provided to *T. californicus* in laboratory cultures, including *Platymonas* (=*Tetraselmis*)(Lear and Oppenheimer, 1962), *Oscillatoria*, Rat Chow® (Huizinga, 1971), boiled wheat, unicellular algae (Lazzaretto et al., 1990) and commercial fish food or multigrain bread (see Chapter 4) Surfaces for microflora growth are provided *in situ* by the incised and pitted bedrock which forms the supralittoral pools, by the surface of encrusting algae, or the longer filaments of algae such as *Enteromorpha compressa* and *Scytosiphon lomentaria*. The small size of *C. trichotoma* filaments (up to 1.0 x 0.2 mm) may possibly be unsuitable for the growth of the particular microflora *T. californicus* may browse.

Effect on Recruitment: The effect of chlorophytic algae on immature (stage N-I to N-VI) *T. californicus* is difficult to discern. In the lab, the results may be biased by the fragility of the eggs and damage in the handling process. In the field, nauplii are very hard to find and may be underrepresented in sampling. While nauplii appear to be comparatively unaffected by *C. trichotoma*, the generally lower tidal elevation of these pools may result in more frequent flushing by wave and tidal inundation, as well as the enhanced potential for filtration or grazing by the increased numbers of sessile and motile organisms occupying pools less frequently emmersed at low tide.

Chemically-Mediated Behavior: Frequently, species gregariousness, the palatability of a food item or suitability of an attachment surface may be determined by the recruitment or "pre-conditioning" of microorganisms (e.g., ZoBell and Allen, 1935;

Ryland, 1959; Crisp and Meadows, 1962, and the citations in that study; Shaw, 1994). Chemical exudates may even determine substrate selection to a greater extent than more obvious surficial features such as form or texture (Crisp and Meadows, 1962). However, fluid flow may reduce the diffusive influence of a chemical secretion to that of a boundary layer narrower than the diameter of a single larva, hence larvae may have to physically touch a given surface before detecting the exudates permeating it. Although the sense organs of very small organisms may be too close together to detect the source or direction of a chemical emission, behavior may still be elicited if a suitable threshold concentration is surpassed (Crisp and Meadows, 1962).

From the current microcosm results, the presence of *C. trichotoma* appears to particularly affect the copepodite stages (C-I to C-VI) of *T. californicus* populations. Laboratory microcosms with *C. trichotoma* provided a lower overall number of surviving individuals, while natural *C. trichotoma* pools retained lower proportions of gravid *T. californicus* females. It may also be possible that the 'toxicity' of food resources are a relative consideration, determined by the acclimation of a short-lived organism to the conditions in which it is reared.

If *Cladophora trichotoma* does produce some compound which is unpalatable, toxic to, or metabolically incompatible with *T. californicus*, a similar response is not noted in littorines, which are found more abundantly in *C. trichotoma* pools than in either of the other pool categories investigated. While a lesser degree of desiccation and more abundant vegetation undoubtedly enhances the suitability of lower pools for littorines, this observation does not support the conclusion that *C. trichotoma* produces some generic compound intended to reduce grazing pressure. As described in Shaw (1994), a true anti-feedant, while acting principally to reduce grazing pressure, is not necessarily lethal to the grazing organism. Two observations in the current study then contradict the traditional designation of *anti-feedant* for the agent potentially produced by *C. trichotoma*: 1) the agent does not apparently inhibit the presence (hence potential grazing pressure) of

grazing meiofauna such as littorines; and 2) the agent exhibits a distinctly lethal effect on at least some life-history stages of *T. californicus*. The apparent deleterious effect of *C. trichotoma* turfs on *T. californicus* abundance may alternately or additionally be the result of the kind of microflora which better grows on *C. trichotoma* filaments (see above), or an indirect physiological reaction of *T. californicus* to *C. trichotoma* exudates. Until a more complete isolation and analysis can be performed, the term *crustacean deterrent* may better describe this agent.

CONCLUSIONS

The supralittoral harpacticoid copepod *Tigriopus californicus* does not maintain populations in splashpools containing the macroalga *Cladophora trichotoma*. Copepod populations *in situ* may be culled by incidental littorine grazing in *C. trichotoma* pools, or by enhanced wave action on these pools, which are of a slightly lower tidal elevation. Alternately, the opportunistic *C. trichotoma* may overgrow or interfere with the substrata which ordinarily provide a food source (benthic diatoms and bacteria) for *T. californicus*.

The results of the current study additionally suggest that *C. trichotoma* may emit a substance which is particularly noxious to the adult copepods. Among field sites with equivalent location and elevation, degree of wave exposure, pool volume and algal percent-coverage, those pools containing *C. trichotoma* retained significantly fewer adult *T. californicus*; a trend which was also reflected in laboratory microcosms. However, the overall influence of such an agent, if extant, is countered by the apparent lack of a similar effect on the survival of the early life stages, as observed in laboratory microcosms. The observed absence of *T. californicus* in pools which contain *C. trichotoma* appears to be principally the result of deleterious effects on the adult stages, since maintenance of the population is ultimately dependent on the reproductive success of mature individuals.

CHAPTER 3: DESICCATION RESISTANCE IN *TIGRIOPUS CALIFORNICUS*

INTRODUCTION

Media vita in morte sumus

("In the midst of life we are in death")

— ST. GALL MONKS

The existence of dormant or suspended life-history stages among crustaceans is not uncommon; the most obvious example is the marketing of freeze-dried brine shrimp (*Artemia* spp.) as "sea monkies" and wind dispersal of dormant *Artemia* eggs is noted in Brown and Gibson (1983). The literature specific to the harpacticoid copepod genus *Tigriopus* includes several accounts of ostensibly re-animated individuals. Fraser (1935) described free-living *T. fulvus* individuals arising from a bottled water sample which had been sealed for more than 18 months. Fraser (1936) translated the description of Issel (1914), that

> "as soon as the density of the water reaches a certain degree the copepod *T. fulvus* falls into a state of apparent death, from which it can awake even after a very long time and regain normal activity when the water is sufficiently diluted."

This observation was tested experimentally by Ranade (1957), who described the "state of apparent death" (p. 119) in *T. fulvus* at salinities in excess of 90‰; a condition which could be reversed by transferring the organism to lower salinities. Ranade (1957) also found a positive correlation between exposure to higher salinities and the lethal temperature for *T. fulvus*. Egloff (1966) found all life-history stages of *Tigriopus californicus* to endure 100% relative humidity for up to 30 minutes. Further, although egg sacs survived equally well at 60% relative humidity, nauplii and adult survival were reduced by more than 50% over the same duration. Kasahara and Akiyama (1976)

cursorily described the dormancy in adult stages of *T. japonicus*, however Vittor (1971) found none of *T. californicus*' life-history stages able to survive prolonged desiccation. Conversely, Dybdahl (1994, p. 114) stated that *T. californicus* "lacks desiccation-resistant dormancy or diapause stages," and that 35% of pools may experience *extinction* over six to eight weeks (italics mine), but cites no conclusive evidence for these assertions. Dybdahl (1994, p. 115) also reported the presence of *T. californicus* in "a quiescent state" in moistened rock crevices, a behavior also described for *T. fulvus* by Ranade (1957).

Uniformly, casual reports of desiccation resistance in *Tigriopus* omit crucial information needed to interpret the possible mechanisms involved. Specifically, this includes: 1) a description of water conditions (volume, temperature, salinity or microflora present); 2) the life-history stage(s) involved; or 3) the time interval over which re-animated activity is observed. The latter two observations are critical to understanding the mechanism of the copepod's dormancy: At 20°C, *T. californicus* requires about 10 days to mature from egg to the first copepodite (C-I) stage and a further 11 days to mature to the C-VI stage adult (Chapter 4). Hence, if nauplii (stages N-I to N-VI) are observed within a few days of splashpool re-hydration, the existence of dormant or encysted eggs is suggested; if more mature (C-I to C-VI) stages are observed, the organism's propagation is likely provided by suspended copepodites or adults.

The average occurrence of *T. californicus* is in splashpools at a level 3.6 m above mean water level (MWL), therefore only infrequently influenced by tidal activity and storm waves. The pools typically provide a large surface area and are 2 to 25 L in volume with a "water column" of 5 to 15 cm (Chapter 1). From Chapters 1 and 2, macroalgae common to the supralittoral zone in Barkley Sound include *Cladophora trichotoma*, *Scytosiphon lomentaria/Ralfsia pacifica* and *Enteromorpha compressa*, *E. intestinalis* and *Hildenbrandia* spp. The filamentous *Scytosiphon* and *Enteromorpha* may provide a source of dissolved organic material and naviculoid diatoms for *T. californicus*, or a refuge from predation or exposure to the elements.

Shallow, small volume pools are more directly influenced by atmospheric - rather than oceanographic - processes, and air temperature can provide a reasonable estimate of pool water temperature (e.g., Egloff, 1966, but see Morris and Taylor, 1983). At the same time, orientation, aspect, shading and rock coloration all provide pool-specific water properties and responses to evaporation, and replicate field sites must be selected carefully (Metaxas and Scheibling, 1993).

Within such a severe, highly variable, and discontinuous habitat, the distribution and occurrence of *Tigriopus californicus* is expectedly irregular or patchy. Although conditions will vary with season and location, complete evaporation of these pools or the decimation of a resident *Tigriopus* population by wave wash are undoubtedly frequent occurrences. Harris (1973) estimated the life span of *T. brevicornis* to be 55 days at 15°C, while Itô (1970) provided a longevity estimate of 70 days for *T. japonicus*. Vittor (1971) derived an estimate (to 10% survival) of 130 ± 14 days at 15°C for *T. californicus*, a value which decreased to *ca.* 80 days at 25°C. The same study provided a generation time of 32 days at 15°C, which reduced to 18 days at 25°C. It is therefore easy to speculate that any given splashpool may evaporate at least once, and perhaps several times, over the course of a single copepod generation. See Chapters 4 and 5 for a more detailed discussion.

Vittor (1971) and my own observations have not found *T. californicus* in nearshore plankton samples, however accurate sampling of possible "source" populations from such dynamic coastlines is not easily done. For a copepod, inter-pool dispersal, migration, or simply being deposited from the coastal maelstrom into a basin which provides food resources as well as sufficient refuge must prove equally daunting (see Chapter 1). With these considerations in mind, the chapter study attempts to quantify the ability of *T. californicus* to tolerate desiccation and thus demonstrate a plausible mechanism for *intra*-pool colonization following intervals of complete evaporation. Such

a mechanism would also account, in part, for the observed incidences of outbreeding depression and genetic heterogeneity between outcrops (per Burton, 1990; Brown, 1991).

MATERIALS AND METHODS

Field Sites: All pools were selected from tagged sites monitored in 1994 and 1995 on Helby Island, British Columbia (Lat. 48°51'N: Long. 125°10.5'W), situated in southeast Barkley Sound (Figure 1.1). From these, 12 pools were selected using stratified random sampling, for: 1) similarity in intertidal elevation (between 4.0 and 4.5 m above MWL); 2) similarity of exposure (arbitrarily based on orientation and available wind breaks), and 3) the presence of *Tigriopus californicus* in the dried substrate material. All pools were within 60 m of each other and had completely evaporated (dry to the touch) following four to five days of warm weather, calm conditions and an absence of tidal inundation. Given the proximity and similarity of the pools selected, and lacking any observations to the contrary, similar atmospheric influences and drying periods for all replicates was assumed. Rates of evaporation for all pools were calculated by measuring the depth and perimeter of the pools each day using a consistent set of landmarks. Except for intermittent onshore winds, atmospheric conditions remained consistent during the experiment: no cloud cover, precipitation or tidal inundation and a mean air temperature of 12.7°C.

Six pools contained dried mats of the green macroalgae *Enteromorpha compressa* (Linnaeus) Greville (Guberlet, 1956), and six contained deposits of mixed sediment comprised of detritus, phytobenthos and inorganic material. Three pools of each substrate type were then hydrated using collected rain water (average volume 8 L, salinity 0.8‰ at 15°C) and three with natural sea water passed through a 100 μm filter (average volume 7 L, salinity 31.4‰ at 15°C) and observed for seven days. Water was drawn from field sites using a 30 mL pipette (sampled volumes were replaced), and the number

and stage of copepods in each sample determined using a dissecting microscope and identification key (Monk, 1941, and Chapter 5).

Laboratory Treatments: Concurrent with the field manipulations, samples of dried substrate material were taken from the same pools and allocated to an equivalent number of laboratory beakers (microcosms) and hydrated with 200 mL of either rain water or filtered sea water from the same sources. Due to availability, the average dry weight of *E. compressa* provided was 3.4 g, and of flaked sediment was 0.5 g per treatment.

Microcosms were maintained, uncovered, in a sheltered, outdoor location and observed for seven days, or until no further response was noted. Culture flasks are usually loosely covered to reduce evaporation; however none of the microcosms experienced significant evaporation, and provided a better comparison to field conditions. Enlivened copepods were removed from the microcosms each day, narcotized by 10% dilution with carbonated water (Gannon and Gannon, 1975) and identified by key as male, female, copepodites, or nauplii. Copepods were then monitored in a separate flask to determine the net increase in individuals from each treatment after seven and 14 days. Copepods which still did not respond to gentle agitation were counted and identified, as above, to provide a census of the source population (i.e., the total number of copepods suspended in each dried substrate sample; Table 3.1).

A quantity of each substrate material was also retained at room temperature for a further 10 days, providing a sample of suspended copepods which had not seen any moisture for 14 days (= four days of field evaporation, then 10 days sequestered in the lab), or approximately one tidal cycle.

Using the same methods, dried samples were also re-hydrated using ordinary tap water. Several trials were also performed using available dried algal material which had been stored for up to 15 months. Individuals which were successfully enlivened were either: 1) collected and dried again (to the touch) to test for possible repeated animation

response; 2) retained and observed in laboratory culture; or 3) sacrificed with 5% formaldehyde solution and examined to confirm identifications.

Treatments were compared for: 1) abundance of copepods in source material; 2) percentage of copepods re-animated; and 3) net gain in individuals using a one-way repeated measures Analysis of Variance (ANOVA). Where treatments differed significantly ($\alpha = 0.05$; $P < 0.1$), a Student-Newman-Keuls analysis was performed on all pair-wise multiple comparisons (Zar, 1984; Jandel, 1994).

RESULTS

Calculations derived from the field sites used in this experiment yielded an average value of 2.3 $L \cdot m^{-2} \cdot day^{-1}$ for surface evaporation under relatively calm conditions. This value increased to 3.4 $L \cdot m^{-2} \cdot day^{-1}$ under the influence of wind.

The re-animation response of *T. californicus* under conditions of rain water and sea water addition are summarized in Tables 3.1 and 3.2, and Figure 3.1. Overall, the treatments showed consistent results between field pools and laboratory microcosms. The samples treated with either rain water or sea water, containing *Enteromorpha* or mixed sediment did not differ between field pools and cultures.

Source Material: The dried treatments containing *Enteromorpha* showed a similar abundance of individuals per gram of substrate as sediment treatments (576 copepods $\cdot g^{-1}$ and 494 copepods $\cdot g^{-1}$, respectively). Whether this was due to: 1) copepod attraction to a potential food source or retained moisture; or 2) the number of individuals in the original (pre-evaporation) population could not be determined. There was also no significant difference in the number of individuals retained by each sediment type, as compared between samples used in the laboratory microcosms and samples taken separately from the field sites.

TABLE 3.1. *Tigriopus californicus* response following re-hydration of dried substrate material with either rain water or filtered sea water. Percentages are derived from the proportion of individuals enlivened per number of individuals present per gram of substrate material. Numbers in parentheses refer to the total number of individuals enlivened per the total number counted for each treatment type. Results tabulated for $n = 3$ pools and $n = 3$ microcosms.

Substrate / Water Type	***T. californicus* life history stage**	**% re-animated (#/counted) from Field Pools**	**Laboratory Culture**
Enteromorpha, sea water hydration	Ovigerous female	35.68 (76/213)	31.82 (7/22)
	Male	20.62 (40/194)	7.07 (13/184)
	Female	17.06 (29/170)	7.32 (9/123)
	Copepodite Stages	21.33 (16/75)	20.00 (1/5)
	Nauplii/egg	20.00 (2/10)	33.33 (1/3)
	Overall	24.62 (163/662)	9.20 (31/337)
	S.E.	7.31	12.70
	Max. response on Day	2	1
Mixed Sediment, sea water hydration	Ovigerous female	22.69 (54/238)	10.42 (10/96)
	Male	14.34 (74/516)	8.82 (12/136)
	Female	26.03 (38/146)	11.11 (4/36)
	Copepodite Stages	55.00 (22/40)	0.00 (0/10)
	Nauplii/egg	14.29 (8/56)	0.00 (0/10)
	Overall	19.48 (196/1006)	9.03 (26/288)
	S.E.	16.76	5.60
	Max. response on Day	3	1
Enteromorpha, rain water hydration	Ovigerous female	2.17 (6/276)	7.41 (6/81)
	Male	1.76 (6/341)	5.96 (18/302)
	Female	5.71 (6/105)	3.55 (6/169)
	Copepodite Stages	0.00 (0/16)	12.50 (1/8)
	Nauplii/egg	0.00 (0/4)	0.00 (0/1)
	Overall	2.43 (18/742)	5.53 (31/561)
	S.E.	2.34	4.64
	Max. response on Day	2	5
Mixed sediment, rain water hydration	Ovigerous female	19.25 (41/213)	0.00 (0/10)
	Male	9.80 (14/143)	0.00 (0/92)
	Female	14.61 (26/178)	0.00 (0/24)
	Copepodite Stages	22.22 (2/9)	0.00 (0/4)
	Nauplii/egg	0.00 (0/8)	0.00 (0/0)
	Overall	15.06 (83/551)	0.00 (0/130)
	S.E.	8.74	0.00
	Max. response on Day	1	N/A

TABLE 3.2. Net increase in *Tigriopus californicus* life-history stages after one week of observation. Since the mass of dried material and overall population response in field pools could not be accurately determined, the values expressed are from the laboratory microcosms only. Net increase is expressed as the number of individuals reared per gram of dried substrate.

Substrate / Water Type	*T. californicus* life history stage	Net increase (# of individuals per gram of substrate material) in 1 Week
Enteromorpha, sea water hydration	Ovigerous female	2.4
	Male	4.2
	Female	3.1
	Copepodite Stages	0.3
	Nauplii/egg	0.6
	Mean	3.2
	S.E.	2.1
Mixed Sediment, sea water hydration	Ovigerous female	3.4
	Male	2.6
	Female	1.4
	Copepodite Stages	0
	Nauplii/egg	0
	Mean	1.5
	S.E.	1.5
Enteromorpha, rain water hydration	Ovigerous female	2.1
	Male	6.0
	Female	2.1
	Copepodite Stages	.7
	Nauplii/egg	0.2
	Mean	2.2
	S.E.	2.3
Mixed sediment, rain water hydration	Ovigerous female	0
	Male	0
	Female	0
	Copepodite Stages	0
	Nauplii/egg	0
	Mean	0
	S.E.	0

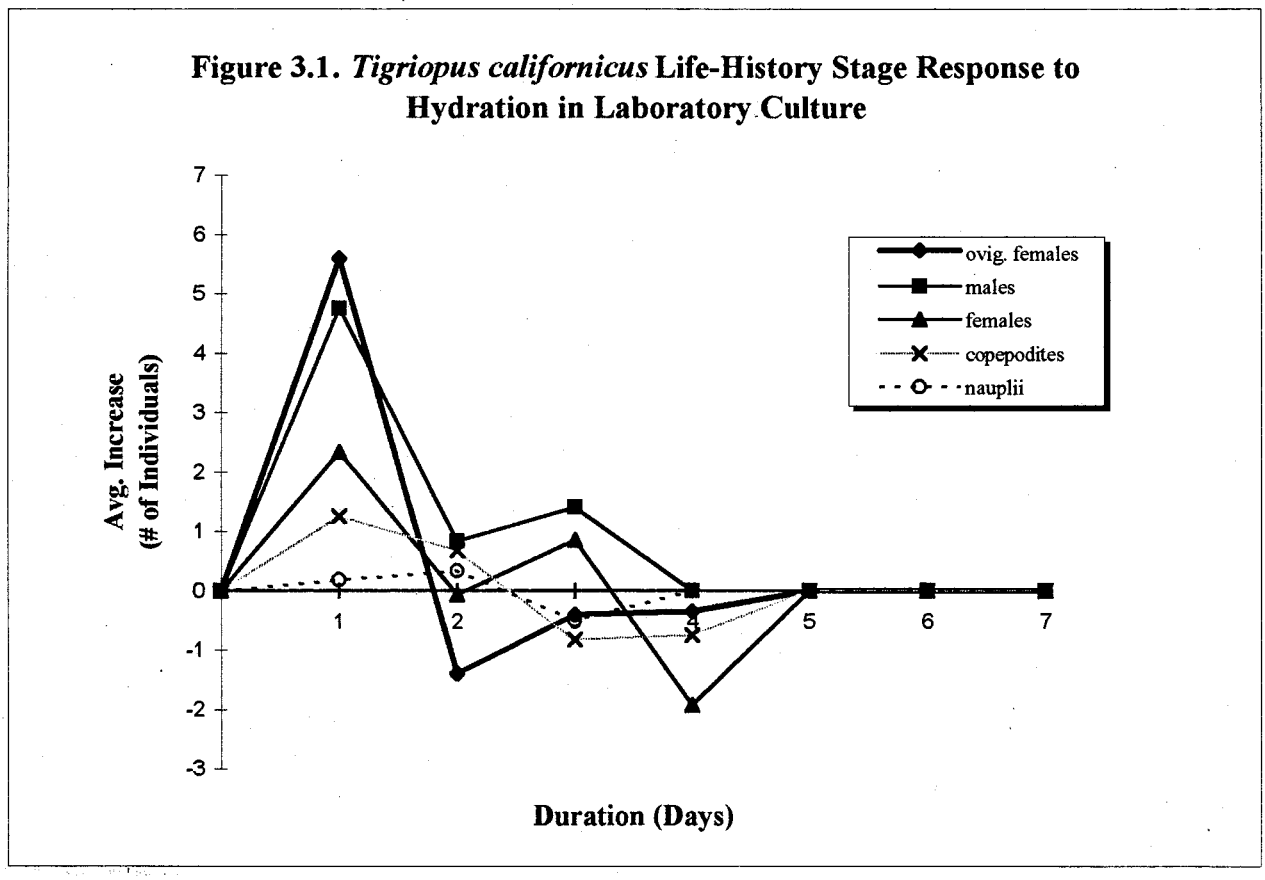

FIGURE 3.1. *Tigriopus californicus* life-history stage response to hydration in laboratory culture. The response between substrate types and field-versus-laboratory samples did not differ statistically, and the *in situ* population response could not be accurately monitored. For clarity, results are presented as the mean response of all laboratory treatments, for each life-history stage.

Percent Re-animation: The sediment/sea water treatments showed a significantly higher percentage of animated individuals, a result which could have been due to an under-sampling of 'source' individuals in the laboratory specimens, or (in one instance) the accidental introduction of individuals from adjoining pools which had not evaporated.

Net Gain of Individuals: The *Enteromorpha* treatments showed a higher percentage and net gain of individuals, particularly with re-hydration using sea water. However, the net increase was not significant with the one-way ANOVA at $\alpha = 0.05$; $P < 0.1$). Overall, the presence of sea water appeared to have a more significant influence on the response of cultures than the substrate type.

Using the abbreviations L (lab culture), F (field) / E (*Enteromorpha*), S (sediment) / SW (sea water), RW (rain water), the re-animation response for all treatments, scaled for volume and mass of sediment material and ranked from lowest to highest was:

L/S/RW < F/E/RW < L/S/SW < L/E/RW < F/S/RW < L/E/SW < F/S/SW < F/E/SW

Immediacy of Response: From Figure 3.1, the maximum re-animation response in culture copepods occurred within 24 hours for all life-history stages, but particularly ovigerous females and adult males. A second net increase was noted during Day 2-3, with adult stages demonstrating similar gain/loss responses over the first five days. No further enlivened individuals were noted after Day 5.

Additional Results: Enlivened individuals were not observed from the dried samples stored an additional 10 days (i.e., at least 14 days since last moistened). Whether this was the result of eventual death of the copepods or the quality of the dried samples could not be determined.

Attempts to re-animate dried samples using ordinary tap water were unsuccessful. Were even a very few enlivened individuals noted in these trials, a lack of bacteria in the water might be suggested; a more obvious explanation is that the chlorine in the water was deleterious or lethal to the copepods.

Re-hydration of dried algal material which had been shelf-stored was also unsuccessful, probably due to: 1) an insufficient number of suspended copepods in the samples available; and 2) the eventual, complete death of the copepods.

Several attempts were also made at air-drying enlivened individuals, then re-hydrating them again in either fresh or saline water. Only 2 of 27 individuals (7%) were successfully revived in this way (one ovigerous female and one immature copepodite); this was probably due to the smaller proportion of copepods tested for repeated response.

DISCUSSION

Using *Tigriopus californicus* populations as an example, the results of the current study reveal at least three significant caveats for the study of populations of ephemeral splashpools:

1. Data collected and presented as individuals per volume sampled will not be sensitive to the volumetric history of the pools. Since the pool volume may change rapidly (due to precipitation, runoff or wave exposure), or gradually (by evaporation), each sample can only be considered a snapshot of ***in situ*** conditions. Increased densities of individuals per volume sampled over time may not represent a 'bloom' in actual numbers, but rather only a change in pool volume. A preferred method would present the data as individuals per unit pool volume at the time of sampling;
2. Calculations of production, immigration, emigration, gene flow or metapopulation extinction must be sensitive to the presence of individuals re-animated from a suspended state. As an average over all our treatments, such re-animation may occur to the extent of 10.7 ± 8.5% of all individuals; and
3. Although the re-animation response appears to be quite consistent over all life-history stages, the net increase in individuals may be biased by disproportionate representation of certain life-history stages (particularly ovigerous females and adult males) in the source material.

Dybdahl (1994) noted that sufficiently high tides to promote wave re-distribution of supralittoral pool water may only exist one or two days per month. From over a year of our field data from Barkley Sound, an average-sized *Tigriopus californicus* pool is 10.5 L in volume and 0.24 m^2 in surface area (Chapter 1). Based on calculations from the current study on the rate of pool evaporation, and lacking precipitation or tidal infiltration, such a pool would be expected to evaporate completely within 7 to 8 days. Although spring conditions in Barkley Sound are notoriously damp (19.2 cm precipitation, 14 year April average), prolonged dry conditions and high winds can be experienced in all seasons. Thus, the frequency of complete pool evaporation is probably quite high and, depending on the size of the pool, may be experienced by the resident *T. californicus* population as often as four times per generation. Based on the current results, a pool which was re-hydrated as little as once per week could potentially maintain a population of *T. californicus*; two weeks' duration between evaporation and re-hydration would likely result in population extinction (see Chapter 5).

Even low proportions of re-animated copepods may yield enough individuals to establish a new population in a re-hydrated pool. Dybdahl (1994) estimates that 75% of colonizing *T. californicus* populations contain 10 or fewer individuals, an observation similar to those of Vittor (1971). Assuming an average re-animation response of 10.7 ± 8.5% (mean ± S.E.) from all treatments, this would require a source of only 99 dried individuals to produce 10 colonists, although slightly dependent on the gender and life-history stages present in the dried sample. If the same success rate is assumed constant for a second re-hydration (7.4%), a source of 1340 individuals would be required to produce 10 colonists after two evaporations. Both values are within reason for large *Tigriopus* populations locked in the substrate material of evaporated pools: Some concentrated populations have approached 200,000 or more individuals · L^{-1}; in a 7 L pool, this would be over 1000 times the source population required to enliven 10 colonists from two successive re-hydrations. At such densities, an average success rate of

only 7.1 x 10^{-4}% would permit re-animation of a sufficient number of individuals to colonize a pool.

Applying these results, approximately one-half of the re-animated individuals would be ovigerous females or other adult stages (Table 3.3). Under favorable conditions, this would provide a remarkable 'at the ready' potential for releasing eggs and rapid re-colonization from 50% of the colonists. The remaining re-animated individuals would be juvenile stages (copepodites or nauplii), reaching maturity in one to two weeks. The ultimate influence of these juvenile stages would depend upon the frequency of complete desiccation. Further, I observed an average increase of 6.9 individuals · day^{-1} re-animated from the microcosms containing *Enteromorpha* and an increase of 8 individuals· day^{-1} from pools containing *Enteromorpha.* These values could reasonably contribute up to 7% of the calculated increase in living *T. californicus* populations provided by Dethier (1980). Her "0.2 individuals per 15 mL" (p.103) equates to 13 L^{-1} or 107 individuals · day^{-1} in a 7 L pool such as the treatments used in the current study.

The inclusion of individuals from virtually all life-history stages further assures the stability and longevity of the population. Egloff (1966) found all life stages to be present on the carapaces of crabs and proposed this as one possible means that *Tigriopus* might use to move between pools. The reliability of this is doubtful, however, since the crabs may travel to lower or otherwise inhospitable intertidal sites, and are themselves attractive targets for birds and other predators (see Chapter 1). Vittor (1971) described a re-colonization response in *T. californicus* whereby there is a rapid increase in population size from a limited number of colonists. *Tigriopus* copepods are notorious for their fecundity and efficiency of egg production (Egloff, 1966; Burton, 1985, for *T. californicus*; and Comita and Comita, 1966; Harris, 1973, for *T. brevicornis*) and a small number of individuals of differing ages might quickly and effectively re-colonize a pool. From the current results, this process seems to require only sufficient moisture and the provision of an adequate food resource. Also consistent with these results is the

TABLE 3.3. Differentiation of animated *Tigriopus californicus* as potential re-colonizers of hydrated pools. Approximately half of the sample would contain adult individuals, capable of immediate reproduction or egg deposition, while the remainder would be juveniles reaching maturity in seven to 10 days.

T. californicus **Life-History Stage**	**Percentage (± S.E.) Present in Re-animated Sample**	**Potential Response**
Ovigerous Females	17.8 ± 2.02	Immediate deposition of eggs. Production of remaining broods.
Adult Males	11.01 ± 1.57	Insemination of receptive females.
Adult Females	13.64 ± 1.69	Reception of males. Production of eggs from previous insemination.
Copepodites	18.82 ± 2.37	Rapid re-animation response. Maturation within 1 week.
Nauplii / eggs	12.49 ± 2.43	Maturation within 2 weeks. (Possibly less resistant to stress).

observation in other studies that gene flow between neighboring pools of *T. californicus* is much more restricted than would be expected of organisms capable of dispersal living in an unstable or stressful habitat (Burton, 1986, 1990; Brown, 1991).

With the exception of the algae/ rain water treatments, field populations apparently responded better than laboratory populations to re-hydration. Rain water (salinity = 0.8‰) added to dried *Enteromorpha* in our field sites achieved a final salinity of 38.5‰, which compares to the sea water treatments. In contrast to Ranade (1957), the current results suggest that dilution effects alone were not responsible for the re-animation response. Rather, it is probably an artifact of: 1) over-estimating the source population; or 2) under-sampling enlivened individuals in the larger pools containing *Enteromorpha*. It also suggests that with sufficient localized concentrations of salts, bacteria and detrital material, ordinary precipitation may accumulate these substances to produce pool water that approximates sea water in its composition. In other words, whether the moisture is derived from wave action or precipitation, it may ultimately be equally as effective. It is also conceded that the actual dehydration of individuals was not determined. All "dried" individuals were assumed to be equally desiccated by natural conditions, which is doubtfully the case. A more appropriate description of dehydration could indicate changes in individual body volumes following hydration (per Wulff, 1972), however such handling may introduce other sources of error or damage suspended specimens.

The comparatively better response of treatments provided both *Enteromorpha* and sea water may indicate the response of *T. californicus* to higher levels of bacteria, nutrients or trace metals. *Tigriopus californicus* is commonly found in the same pools as some macroalgae, while being entirely absent from pools containing other algal species (Chapter 2). Thriving populations are also observed in pools lacking any macroalgae or sediment. From this, and the observations of Chapter 1, the food source for field

populations is most likely bacteria or benthic diatoms, and both of these food types would be provided either by tidal infiltration or precipitation.

A series of qualitative observations yields the following proposed sequence of events during splashpool evaporation: As the water volume is decreased, the pool's perimeter is reduced and irregularities in the basin may divide the pool into sub-basins. Surviving *T. californicus* congregate in these sub-basins, or take refuge in any moisture-retaining vegetation. At this time, concentrations of individuals exceed 200 mL^{-1} sampled; values one to two orders of magnitude higher than previously published 'high' in situ densities (e.g., Fraser, 1935, for *T. fulvus*; Dethier, 1980, for *T. californicus*; Igarashi, 1959, for *T. japonicus*). At this time, density-dependent responses such as cannibalism, maternal predation on nauplii or retention of egg sacs may predominate, as found in *T. japonicus* (Kahan et al., 1988) and *T. fulvus* (Lazzaretto and Salvato, 1992). The result is an essentially adult population, as the production and survival of young stages is greatly reduced.

As the slight water column evaporates, adults settle out of solution atop the remaining copepodite and naupliar stages, which in turn seek the moisture retained between the larger adults. Copepodites were re-animated the most quickly (within 15 minutes in some instances), perhaps because of their larger surface area-to-body volume ratio relative to mature adults. Adult males and ovigerous females provided the greatest success in re-animation, most likely due to their overwhelming representation in the dried material (up to 62% and 40%, respectively).

Kahan et al. (1988) observed that ovigerous *T. fulvus* females apparently do not drop their egg sacs in response to increased salinity. These authors also observed that culture females sacrificed by a variety of means will release their eggs usually within an hour, and eggs removed from the female will hatch nearly immediately. The retention of egg sacs by females in evaporated pools then poses an interesting question: how do the gravid females respond at the moment of their death and, accordingly, release their eggs?

Whether by structural or hormonal modification, the retention of egg sacs by inanimate females may provide one clue as to whether they are suspended or in fact dead.

Tigriopus californicus nauplii sampled from field populations in Barkley Sound are very much reduced from expected abundance in natural populations, which concurs with the observations of Harris (1973) for *T. brevicornis*. Since *T. californicus* nauplii are short-lived (from Chapter 5, about two days for each nauplius stage), they may be very ephemeral in field populations. Cannibalism may further reduce these numbers, and the preference of the nauplii to associate close to the bottom of pools undoubtedly also reduces their representation in samples; whether nauplii are captured by sampling may be a matter of timing (hence improved by an increased frequency of sampling). O'Brien et al. (1988) find the tolerance of *T. californicus* to cupric ion activity to be at a minimum for stages N-I through N-IV, and with the exception of eggs (which showed tolerance intermediate between the naupliar and copepodite stages), there appears to be a gradual, rather than sudden, increase in tolerance to cupric ion activity through to the C-VI adult. If these results are applied generally to pollutants, the carrying of eggs by suspended adults may be one way for the less-resilient juvenile stages to avoid potentially inhospitable conditions at the time of re-hydration. Hence, the retention of eggs by the female may provide some assurance that young will be released only under favorable conditions.

CONCLUSIONS

The copepod *Tigriopus californicus* has demonstrated the ability to recover from retention in evaporated splashpools if the duration of this desiccation does not exceed seven to 10 days. The response to either fresh or saline hydration is nearly immediate, and is observed across all life-history stages, albeit proportionate to the body volume and representation of these stages in the source sample. With the presence of continued moisture and food supply, re-animated individuals appear to be completely viable.

Despite the low overall percentage of recovery observed, the response is likely adequate to promote the re-establishment of populations within pools.

CHAPTER 4: DEVELOPMENT, BODY LENGTH, AND FEEDING OF *TIGRIOPUS CALIFORNICUS* IN LABORATORY AND FIELD POPULATIONS

INTRODUCTION

"Growth is the only evidence of life."

— J. H. NEWMAN (1864)

The natural abundance of harpacticoid copepods, as well as their small size, remarkable fecundity, short generation time, and tolerance to extreme or sudden fluxes in the supporting aqueous medium are attributes that have served to promote their use in a diverse array of experimental applications. Examples specific to *Tigriopus californicus* alone, include evaluations of copepod feeding (Lear and Oppenheimer, 1962; Sullivan and Bisalputra, 1980; Syvitski and Lewis, 1980) and suitability as food for cultured fish stocks (Morris, 1956; Fahey, 1964), response to pollutants or thermal and osmotic stress (Chipman, 1958; Huizinga, 1971; Kontogiannis, 1973; Kontogiannis and Barnett, 1973; McDonough and Stiffler, 1981; O'Brien et al., 1988; Misitano and Schiewe, 1990; Burton, 1991), sex determination and development (Vacquier and Belser, 1965; Egloff, 1966; Palmer et al., 1993), fecundity (Burton, 1985); and genetics (Ohman, 1977; Burton et al., 1979; Burton and Swisher, 1984; Burton 1987,1990; Brown, 1991, to list only a few examples). Indeed, all *Tigriopus* congeners may claim an equal diversity of applications, but a catalog of these is beyond the intent of this thesis.

The development of *Tigriopus japonicus* has been described by Igarashi (1963a, 1963b), and illustrated extensively by Itô (1970) and Koga (1970). Fraser (1936b) and Bozic (1960) document the natural history and taxonomy of *T. fulvus,* respectively, while Comita and Comita (1966) and Harris (1973) provided the benchmark studies for the egg production, growth, and physiology of *T. brevicornis*. Burton (1985) detailed the mating system of *T. californicus* and Huizinga (1971) discussed cursorily the development of

T. californicus and maintenance of the organism in culture. A number of studies have addressed related population-level responses of *Tigriopus* copepods in laboratory culture, including dormancy of life-history stages (Fraser, 1935; Kasahara and Akiyama, 1976), development and brood production (Igarashi, 1960; Takano, 1971, which includes several early citations for *T. japonicus*), and chemically-mediated behavior (Kahan et al., 1988; Kahan, 1992 for *T. japonicus*; and Bozic, 1975; Lazzaretto et al., 1990; Lazzaretto and Salvato, 1992 for *T. fulvus*). A satisfactory description of the life-history of *T. californicus* has not been published, despite the taxonomic description of Monk (1941), studies of field populations by Egloff (1966) and Vittor (1971), and analyses of population genetics by Burton et al. (1979), Brown (1991) and several more recent studies by Burton. Inevitably, assumptions on the species' development are drawn from observations made from its congeners, which may be sufficient for most, but not all, applications. Further, experimental results have frequently been presented with reference only to *adults*, *eggs*, or *larval stages*, with little mention of the life-stages categorically so included. No published studies have yet addressed the development of *T. californicus* under conditions truly representative of the temperate, supralittoral splashpools that are the organism's natural habitat.

The intent of the current chapter is to provide a synthesis of the foregoing studies with my observations on the maintenance of *T. californicus* in culture. The organism's morphological development under laboratory and seasonal *in situ* regimes will be evaluated, with particular consideration of water temperatures and salinity typical of the organism's natural environment.

MATERIALS AND METHODS

Specimens of *Tigriopus californicus* (Baker) were collected from field sites in Barkley Sound (Chapter 1) into 500 mL Nalgene bottles and maintained with the

following technique modified from Huizinga (1971) and Omori and Ikeda (1984): Samples were transferred in their natural pool water into 2 L Erlenmeyer flasks, then either: 1) maintained at 18 - 20°C and 32 - 35‰ to approximate summer conditions; or 2) chilled (cold room or ice bath) at 10 - 15°C and 20 - 25‰ salinity to approximate winter conditions. Temperatures and salinity selected were representative of seasonal conditions for the field sites (see Chapter 1). The volumes of all stock cultures were maintained at approximately 1.5 L by replenishment with distilled, de-ionized water (DDW) to maintain consistency in the levels of bacteria, microalgae, and salt content; a Petri dish or watch glass was placed loosely over the mouth of all flasks to prevent undue evaporation.

Cultures were also inoculated every seven to 10 days with 50 mg of Wardley's Basic Fish Flakes® or a culture of mixed bacteria[1] from the Northeast Pacific Culture Collection (University of British Columbia, Vancouver), as available. While the amount of nutritive material used to support 'summer' and winter' cultures was the same, the seasonal *in situ* splashpool water undoubtedly differed in the taxa and initial abundance of natural bacteria and unicellular algae present (Lee and Taga, 1988; Metaxas and Lewis, 1992; Carli et al., 1993).

To evaluate the organism's development, egg sacs were removed from gravid females and transferred individually to six-well plates kept at room temperature or chilled; water conditions as above. All wells were examined daily with a dissecting microscope or jewelers' glass; after hatching or molting, a selection of individuals (150 eggs, then 50 of each subsequent life-history stage) were removed from each tray and examined for external morphology and size (diameter or maximum length). *Maximum length* is here defined as the straight line distance from the rostrum to the posterior terminus of the caudal rami, or the equivalent position on juveniles (nauplii) where these structures have yet to develop. Molted individuals were then transferred into new wells or sacrificed for

[1] The species composition of this culture was unavailable at the time of this writing.

detailed examination at higher magnification under oil immersion. Slides were prepared following the methods of Omori and Ikeda (1984): specimens were sacrificed with lactic acid and stained for 30 to 60 min in diluted chlorazol black E. Specimens were then rinsed in benzyl alcohol and DDW and transferred to a drop of glycerin for dissection, mounted in Aquitex and preserved on a flat microscope slide with the coverslip sealed with Artmatic clear nail polish.

Tigriopus californicus individuals were collected concurrently from splashpool populations in Barkley Sound and examined for abundance and maximum length of: 1) eggs (including brood size); 2) nauplii (stages N-I to N-VI inclusive); 3) copepodites (stages C-I to C-IV); and 4) mature adults (stages C-IV to C-VI, including gravid females). Samples were drawn randomly in July and October of 1994 and January and May of 1995 from pools retaining the above temperature and salinity ranges over at least three consecutive days. All individuals were either narcotized in 10% carbonated water (Gannon and Gannon, 1975) to facilitate vital examination with a dissecting microscope, or sacrificed for detailed examination using a compound microscope at higher magnification, usually within 12 h of collection.

RESULTS

The results of *Tigriopus californicus* life-history stage development and duration are summarized in Table 4.1. Eggs begin as green spheres, becoming red or dark orange with maturation as the eye develops. Egg sacs are carried in a single brood sac by the gravid female, and eggs usually hatch within 24 h of deposition or removal from the female (slowed by 12 to 24 h in the solution at 10 - 15°C, see Table 4.1). These observations coincide with the observations of Kahan et al. (1988) for *T. japonicus* and Huizinga (1971) for *T. californicus*; but is much more rapid than either the 2.4 days (at 23°C) to 8.2 days (at 10°C) noted by Egloff (1966) for *T. californicus*.

TABLE 4.1. Development of *Tigriopus californicus* in laboratory culture. *Summer* denotes cultures at 18 - 20°C, 30 -32‰ salinity; *winter* denotes cultures at 10 - 15°C; 20 - 25‰ salinity. Supporting media for all treatments was 1.5 L of natural pool water, replenished with distilled, de-ionized water and inoculated with fish flakes or mixed bacterial culture. Parentheses indicate number of specimens observed of each life-history stage. Description of morphology *sensu* Coull (1982).

Life-History Stage		Stage Duration (Days)	Days After Egg Deposition	Body Diameter (μm)	Development
egg	summer	1	< 1	50 - 80	Green color becomes red due to
(56)	winter	2	1-2	50 - 90	microflora and eye development
Nauplius stages					
N-I	summer	1	2	40 - 80	Urosome develops anteriorally
(32)	winter	1	3	40 - 80	
N-II	summer	1	3	50 - 100	First setae on proto-urosome
(28)	winter	1	4	50 - 100	
N-III	summer	2 - 3	6	100 - 150	Begins (observable) feeding and
(26)	winter	3	7	100 - 150	swimming
N-IV	summer	1	7	150 - 200	Enlargement of body;
(22)	winter	1	8	150 - 200	Lateral prosome setae bifurcate
N-V	summer	1	8	200 - 300	Urosome segmentation evident
(25)	winter	1	9	200 - 300	
N-VI	summer	2 - 3	10	200 - 300	Urosome segmentation advances
(25)	winter	3	12	200 - 300	P1, P2 appendages appear
Copepodite Stages					
C-I	summer	2 - 3	13	430 - 460	5 somites + caudal rami;
(18)	winter	3 - 4	16	400 - 420	P3 appendages appear
C-II	summer	2 - 3	15	520 - 550	6 somites + caudal rami;
(15)	winter	3 - 4	20	500 - 530	P1 to P3 appendages complete
C-III	summer	2 - 3	18	650 - 700	7 body somites + caudal rami;
(19)	winter	3 - 4	24	630 - 660	P1 to P4 appendages complete; P5 appendages appear
C-IV	summer	2 - 3	20	740 - 760	8 somites + caudal rami
(15)	winter	3 - 4	28	730 - 760	
C-V	summer	1	21	1100 (males)	Sexual dimorphism occurs;
(23)	winter	1-2	30	1000	Males develop larger A1 antennules and larger body size;
(20)	summer	1	21	1000 (females)	Female P1 may be larger, more
	winter	1-2	30	880 - 1000	developed, female P5 appendage fused, modified for egg clutch;
C-VI	summer	28+	30+	1400 (males)	11 somites + caudal rami
(45)	winter	28+	30+	1300	
(40)	summer	28+	30+	1100 (females)	Female C-VI molt may not occur
	winter	28+	30+	1000 - 1100	without fertilization of C-V

Clutch size was seen to be highly variable in all seasons, particularly in field populations (Figure 4.1). The observed range in clutch size was 12 to 56 eggs. Clutch size for laboratory cultures (52 individuals) was 20 ± 4.2 eggs (mean ± S.E.) at 10 - 15°C and 26 ± 8.1 eggs at 18 - 20°C (mean values rounded to the nearest whole individual). Gravid females from field populations (an additional 87 individuals) had a mean clutch size of 23 ± 6.5 eggs at 10 - 15°C, and 37 ± 10.2 eggs· clutch^{-1} in pools sampled in July and August (61 individuals). Non-viable progeny accounted for 10 ± 9.1% of all eggs (n = 1092) at the lower temperature/salinity and 10.8 ± 7.8% (n = 1837) at the higher temperatures and salinity.

As indicated in Table 4.1, development of *T. californicus* nauplius stages is marked principally by the behavior exhibited, a six-fold increase in size (diameter), and the onset of segmentation of the urosome. The nauplii are nearly transparent except for the eye spot at the N-VI stage. Feeding on particulate matter is not observed prior to the N-III stage, although absorption of dissolved materials through the cuticle or feeding on internal reserves may be possible. Self-directed swimming (auto-locomotion under non-turbulent conditions) is also not observed prior to the N-III stage, which may enhance the susceptibility of the organism to cannibalism or predation during its early life-history. There was also no appreciable difference in the size and morphological development of nauplii under "summer" versus "winter" culture conditions, however the net development of *T. californicus* from egg through stage N-VI is slowed by 2 days overall at the lower temperature/salinity range. The net size of the organism at the N-VI stage remained within the 200 to 300 μm size range under both rearing regimes.

Development of the copepodite stages C-I through C-IV is externally evident by segmentation of the metasome and urosome, with an increase in body length of 50 to 100 μm and the appearance of an additional pair of swimming legs (appendages P_1 to P_5) at each molt. Copepodite development was also observed to be slower at the lower temperatures, adding approximately 1 day to each interval between molts for a net

difference in development time of more than a week from egg to maturation, the C-VI stage. The observations additionally suggest that the stage C-V female may not molt into the C-VI stage *unless* it is fertilized by the male, contrary to the observations of Harris (1973) and Burton (1985). Further, C-V females are usually clasped soon after they molt, and riding may be inhibited if the male cannot clasp the female or implant the spermatophore after the cuticle has hardened. Only trial-and-error attempts at coupling by the male or a chemical secretion associated with the molt may indicate receptivity of the female to clasping. Overall body length of all life-history stages was seen to be more variable at the lower temperature range and in field populations, but did not differ substantively from the size ranges observed in culture (Figures 4.2 and 4.3). Where differences in length were noted, cultured organisms were generally shorter in length than the field specimens, an artifact that may indicate differential food availability, or variation in the overall body size or volume not indicated by a single linear axis.

From the description of Coull (1982), *Tigriopus californicus* exhibits a fusiform compressed body form at maturity; sexual dimorphism occurs at the C-IV stage, when the organism can be sexed by a larger, geniculate A_1 antennule in the male, and a more intricate P_5 swimming appendage in the female, where the basis and endopodite are fused and may protect or serve as an attachment point for egg sacs. The P_1 appendage may also be larger and more setated in the mature female. Characteristic of the generalized harpacticoid plan (Coull, 1982), articulation with the urosome occurring between the fifth and sixth body segments (somites) and the fully-developed A_1 (antennules) are biramous and eight segments in length. The prosome is broader than the urosome and consists of the cephalo-thorax (the three fused, anterior-most somites) and the metasome (the next two body segments, which are generally smaller and restricted in their articulation). A further six somites comprise the urosome in advance of the caudal rami, and the rami may be apparent as early as the C-I stage.

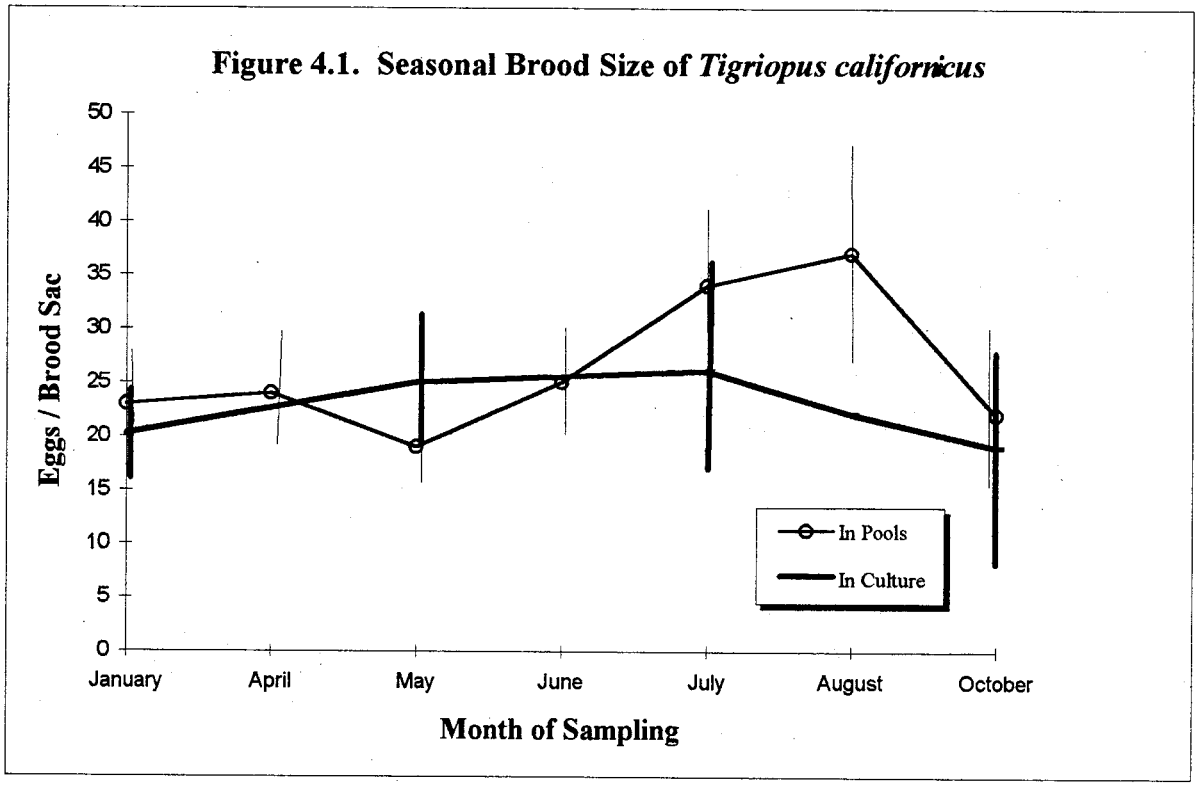

FIGURE 4.1. Seasonal brood size in *Tigriopus californicus*. Mean brood size for 52 gravid females samples from laboratory culture and 87 additional females collected from field populations during the months indicated. Pools were selected with temperature and salinity parameters representative of seasonal mean. Note that data are only available for four months for laboratory cultures, compared to seven months for pool samples. Error bars indicate ± 1 S.E.

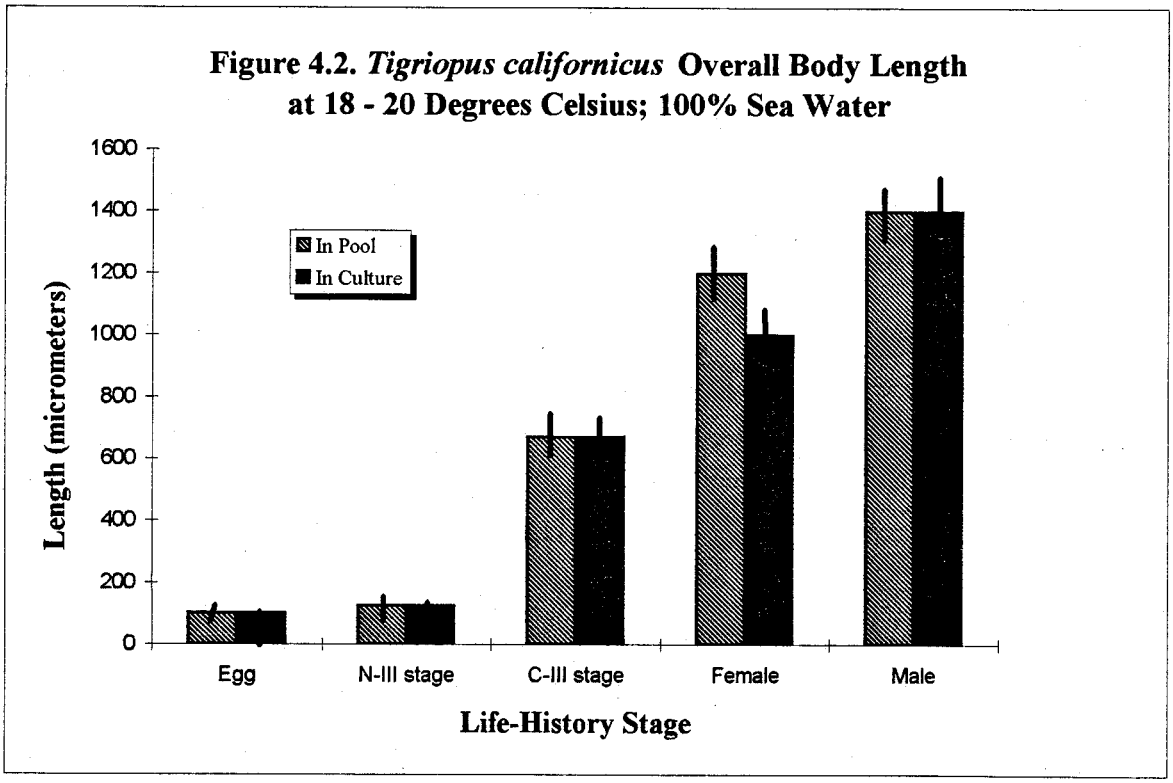

FIGURE 4.2. Overall body length of *Tigriopus californicus* at 18 - 20°C; 100% sea water (30 - 32‰ salinity). For illustration, only the median nauplius (N-III) and copepodite (C-III) stages are presented. Error bars indicate ± 1 S.E. of the mean values for $n = 150$ eggs and $n = 50$ individuals of each subsequent stage.

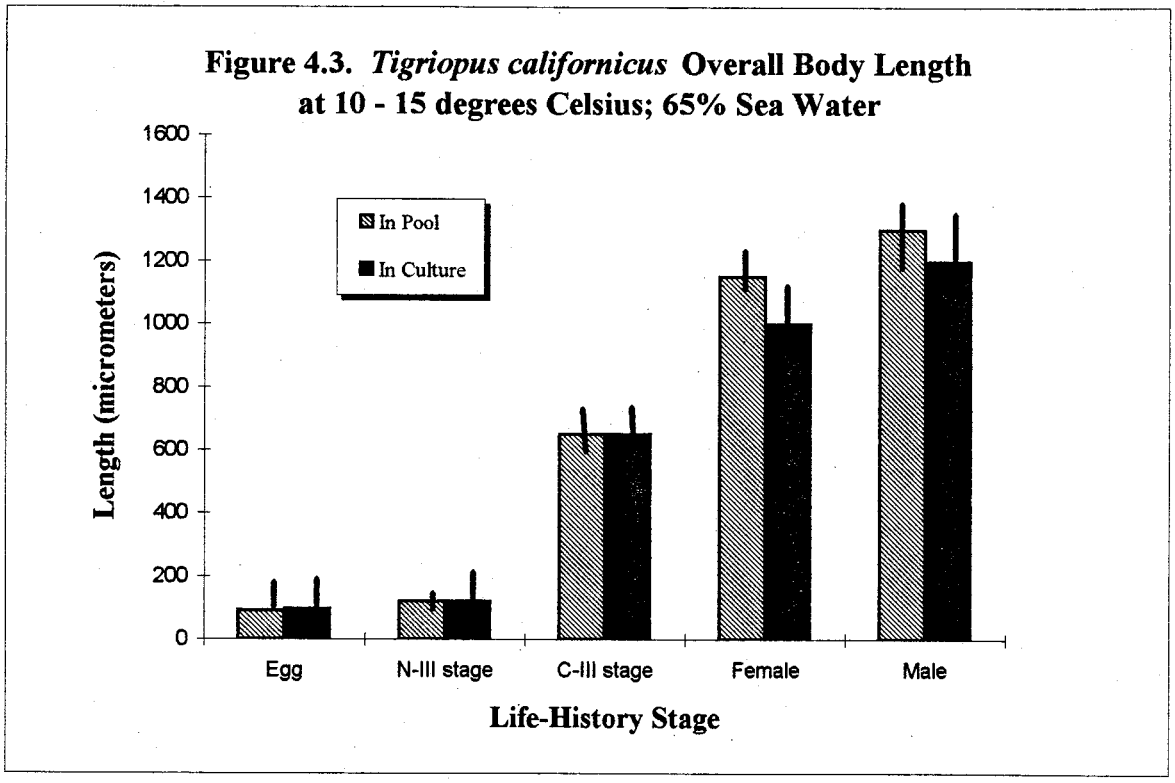

FIGURE 4.3. Overall body length of *Tigriopus californicus* at 10 - 15°C; 65% sea water (20 - 25‰ salinity). For illustration, only the median nauplius (N-III) and copepodite (C-III) stages are presented. Error bars indicate ± 1 S.E. of the mean values for $n = 150$ eggs and $n = 50$ individuals of each subsequent stage.

From Table 4.1 and Figures 4.2 and 4.3, the net size of the mature individuals differed little between the two temperature/salinity ranges in laboratory culture. Culture specimens also did not differ significantly from field specimens collected concurrently during the summer and winter (Student's t-test at $\alpha = 0.05$, $P < 0.20$).

DISCUSSION

Culture Maintenance: Huizinga (1971) maintained *T. californicus* in 20 cm finger bowls, in natural sea water, for one week. As nutritive media, 150 mg of blended Purina Rat Chow® was added every four to seven days; the fluid medium was diluted to 1300 mL with prepared sea water, covered and left at room temperature. Evaporated water was replaced by distilled water, while cultures were split every two to three weeks into sub-samples containing approximately 500 adults and topped up to 1300 mL with artificial sea water. In marked contrast to Huizinga's custodial method, Fraser (1935) reports the retention of *T. fulvus* in a sealed jar of natural pool water for more than a year, and observed activity of the organism days to months after the vessel was re-opened.

Considering the generally high surface-area-to-volume ratio of the copepod's natural habitat, retaining a large interface with the air is essential to provide adequate oxygenation to cultures, particularly those with dense populations. Interruption of this interface, as by oil contamination, has been shown to be deleterious to *T. californicus* cultures (Kontogiannis and Barnett, 1973). Using 2 L Erlenmeyer flasks, covered loosely with a watch glass to prevent evaporation, and replenished gradually with filtered natural sea water at *ca.* 32‰ salinity has yielded the most success for the cultures used for the current study. Such an arrangement provides a generous air/sea water interface while reducing the evaporative loss and occupying a minimum of shelf or bench space. The use of DDW or SOW may be desirable in some applications (including the current one) to maintain the physico-chemical constancy of the solution, however I have not had

success in supporting *T. californicus* cultures for any duration using these more 'sterile' solutions. Cultures have frequently been lost in media that has become too clean (i.e., lacking appreciable microflora).

From the above results, *T. californicus* cultures seem to sustain themselves equally well at room temperature or under refrigeration and a linear correlation between rearing temperature and body length or brood size is not apparent. Takano (1971) found sunlight and storage temperatures in excess of 28°C to be harmful for cultures of *T. japonicus*, and suggests aeration and/or changing the water frequently under these conditions. Huizinga (1971) noted that high ambient light levels caused a filamentous red alga to form that was deleterious to *T. californicus*. I have observed no ill effects on cultures retained under standard fluorescent lighting under either constant light or a 12:12 or 16:8 light:dark cycle.

Feeding: Published accounts of nutritive media for *Tigriopus* include unicellular algae, dried shrimp powder, mulberry leaves, rat food, and bacteria (Table 5.2). In virtually all examples, the "food" provided is not natural to the copepod's habitat, earning the organism the (likely erroneous) designation of a "generalist feeder." *Tigriopus californicus* will feed on any number of items, from commercial fish food to mixed bacterial culture to multigrain bread - any living substance which promotes the formation of bacteria (*cf.* Robinson, 1957; Harding, 1974). For this reason, cultures should be provided with nucleating materials that promote bacterial growth, kept slightly cloudy and decidedly non-sterile without allowing so much bacterial growth or accumulation of nitrogenous wastes that conditions become inhospitable. These observations concur with Huizinga (1971), who noted that *T. californicus* cultures are tolerant to overfeeding and putrescence.

Gilat (1967) referred to *T. brevicornis* as a filter-feeder, without any apparent results to support this claim (noted by Hicks and Coull, 1983). Morris et al. (1980, p. 632) state that *T. californicus* "can filter feed to some extent, like most free-living

TABLE 4.2. Food items used for culture of *Tigriopus* congeners. Additional references for the use of food items for *Tigriopus* cultures are tabulated in the review of Hicks and Coull (1983, p. 138).

Study	*Tigriopus* species	Food Provided (as cited)
Fraser, 1936b	*T. fulvus*	*Nitzschia closterium*
Takeda, 1939	*T. japonicus*	dried, powdered shrimp
Hanaoka, 1940	*T. japonicus*	diatoms
Provasoli et al., 1959	*T. japonicus*	*Rhodomonas* + *Isochrysis* *Platymonas* + bacteria *Chroömonas* + vitamins
Lear and Oppenheimer, 1962	*T. californicus*	*Platymonas (=Tetraselmis)*
Vacquier and Belser, 1965	*T. californicus*	*Platymonas (=Tetraselmis)*
Comita and Comita, 1966	*T. brevicornis*	*Phaeodactylum triconutum*
Egloff, 1966	*T. californicus*	*Platymonas (=Tetraselmis)*
Shiraishi, 1966	*T. japonicus*	bacteria-free algae
Koga, 1970	*T. japonicus*	*Chlorella*, beer yeast, processed trout food
Huizinga, 1971	*T. californicus*	Purina Rat Chow, *Chlorococcum, Oscillatoria,* *Oxyrrhis, Euplotes*
Takano, 1971	*T. japonicus*	*Cyclotella, Phaeodactylum,* *Nitzschia*
Harris, 1973	*T. brevicornis*	centrifuged natural sea water (35 ‰, 500 μgN/L)
Rothbard, 1976	*T. japonicus*	*Ulva petrusa*
Watanabe et al., 1978	*T. (japonicus)*	baker's yeast, soy cake
O'Brien et al., 1980	*T. californicus*	fish food
Lee and Hu, 1981	*T. japonicus*	*Chlamydomonas*
Vilela, 1984	*T. brevicornis*	*Platymonas (=Tetraselmis),* *Nannochloris,* fish flakes, vegetables
Kahan et al., 1988	*T. japonicus*	wheat germ, natural algae.
Lee and Taga, 1988	*T. japonicus*	*Acinetobacter* bacteria
Lazzaretto et al., 1990	*T. californicus* *T. fulvus* *T. brevicornis*	boiled wheat, unicellular algae
Pavillon et al., 1992	*T. brevicornis*	*Tetraselmis cordiformis*
Palmer et al., 1993	*T. californicus*	*Isochrysis*, fish food.

copepods, but is primarily a browser [on] algae and detritus." The description of filter-feeding is used again by Huizinga (1971) and Harris (1973), although the latter reference discusses filtration only in regard to removal of phytoplankton cells. In comparing the feeding appendages of *T. californicus* with those of *Acartia tonsa*, Egloff (1966) asserts that *T. californicus* cannot be a filter feeder, since the plumose setae of its mandibular palps and first maxillae are poorly designed for generating feeding currents or straining water. From Egloff (1966, p. 11) the coxa of *T. californicus* has a strong cutting edge, with a small basipodite and a long endopodite; a similar clarification is made by Itô (1970), and Sullivan and Bisalputra (1980) also suggested that the setae of the mandibles of *T. californicus* function in mastication, rather than filtration. Syvitski and Lewis (1980) describe *T. californicus* feeding on particles 0.5 to 50 μm in diameter, some 20 times smaller than previously noted for the organism, however at the low Reynold's numbers typically experienced by these microcrustaceans, setae on feeding appendages may indeed operate more akin to paddles than filtering sieves. In stock culture preparations, natural sea water is typically filtered at 0.45 μm, which would prevent the passage of most particles of this size range into the stock cultures. Fraser (1936b) and Itô (1970) provide more appropriate descriptions of *Tigriopus* feeding, the latter study describing surface browsing as the means of feeding in *T. japonicus*. From the excellent review of Hicks and Coull (1983), food acquisition in *Tigriopus* species might best compare to the prey-crusher variety of feeding described in Marcotte (1977).

A census of the gut contents of *T. californicus* by Egloff (1966) revealed the dietary items to be (in order of abundance and not further specified): 1) diatoms; 2) green and cyanobacteria; 3) filamentous green algae; and 4) nauplii and copepodite exoskeletons. Huizinga's (1971) census of gut contents includes: 1) the green alga *Chlorococcum*; 2) the cyanobacterium *Oscillatoria*; 3) the dinophyte *Oxyrrhis*; and 4) the protozoan *Euplotes*, with each having been cultured on the blended commercial rat food provided as a nutritive media.

With any census of gut contents, the designation of "preferred" food must be tempered with considerations of relative abundance or possibly noxious taste of alternate dietary items. Although *T. californicus* is capable of cannibalism, only diatoms and bacteria alone may be fed upon preferentially, while the remaining materials are ingested by happenstance. The amount of detritus, macroalgae, and other copepods that are consumed will therefore correspond with the amount of sediment or detrital material present, and the density of the copepod population. Egloff (1966) proposes cognitive predation by female *T. californicus* on its own nauplii, and Lazzaretto and Salvato (1992) discuss cannibalism in *T. fulvus* at higher population densities (in excess of 20 individuals $\cdot$ mL^{-1}).

In contrast to several feeding studies that suggest mixed algae is the staple food resource of harpacticoids (e.g., Lear and Oppenheimer, 1962; Shiraishi, 1966; Battaglia, 1970; Vilela, 1984), marine bacteria alone may provide a sufficient food resource for *Tigriopus* species *in situ*, in accordance with the laboratory results of Provasoli et al. (1959); Gilat (1967); Hanaoka (1973); Itoh (1973); Rieper (1978; 1982) and Carli et al. (1993). Lee and Taga (1988) found 10^6 cells $\cdot$ mL^{-1} of *Acinetobacter* spp. to be ideal for the development of all life-history stages of *T. japonicus*, a bacterial concentration representative of bacteria levels in the splashpools for that study (see General Discussion). Alternately, Itoh (1973) provided an estimate of 0.31 - 1.02 µg dry bacteria $\cdot$ day^{-1} for *T. japonicus*, while Rieper (1978) provided a more general estimate for harpacticoids of 2.06 - 7.07 µg dry bacteria $\cdot$ day^{-1} or 1 - 3.5 µgC$\cdot$ $copepod^{-1}\cdot$ day^{-1}. From Khalov and Yerokhin (1971) and Carli et al. (1993), the bacteria found naturally in pools and in association with the cuticle of the copepods may also assist in the uptake of dissolved organic matter through the cuticle (but see Anderson and Stephens, 1969).

Development of Life-History Stages: Tigriopus californicus apparently exhibits the "typical" harpacticoid development (Hicks and Coull, 1983), molting through six nauplius and six copepodite stages (including the adult) after hatching from the egg.

Although Harris (1973) identifies six copepodite stages for *T. brevicornis*, Huizinga (1971) identifies only four naupliar and four copepodite stages plus the adult stage for *T. californicus*. Sexual dimorphism based externally on the A_1 antennule (males) and flattened P_5 baseoendopodite (females) agrees with the distinction provided by Monk (1941), Egloff (1966), and the observations of Burton (1985).

Egloff (1966) also suggested that body size and coloration may be used to differentiate the sexes of *T. californicus*, however these characters are likely dependent on the diet and thermal/haline history of the culture. In the advanced life-history stages (copepodites and mature adults), the characteristic orange or reddish coloration of *T. californicus* has been observed to coincide with the florescence of microflora in the gut (*cf.* Rieper, 1982). Though the organism does not begin feeding until the N-III stage, it may be possible that some of the microflora is transmuted to the egg sacs as they ripen by the female.

While I have observed very little variation or net difference in final body length between summer and winter conditions, changes in osmotic conditions may produce swelling or shrinkage of the copepod's cuticle, thus changing the body's size or volume. Preparation techniques may also promote shrinkage or distention of specimens, and so a technique which considers changes in the overall body size or body volume (e.g., Wulff, 1972) would be more appropriate than recording length parameters if a more detailed determination of somatic growth is intended.

The use of a range of 2 to 5°C for each culture is justified in being more representative of microscale changes in pool temperatures *in situ*, rather than the typical method of holding this variable constant. The thermal or saline 'history' of the pools (i.e., conditions prior to the time of sampling which may have been greatly dissimilar to the those used for culture), if present, appear to have had little effect on the net size or rate of development of the cultures ultimately produced. While closely representative of the seasonal conditions in Barkley Sound, the range of temperatures used in the current study

to differentiate summer and winter cultures may not have been distinct enough to promote differential growth rates or body length.

An overall slowing of development was observed at the lower temperatures (9 days overall at 10 - 15°C), but did not record increased incidence of egg mortality with either temperature or culture source. Egloff (1966) noted enhanced egg mortality at less than 10°C and greater than 25°C, which are potential but infrequent temperature extremes in our field sites. The total development time (egg to adult) for *T. californicus* calculated by Huizinga (1971) is 18 - 21 days at 23°C; Egloff (1966) reported 16.5 days at 23°C and 27.5 days at 15°C. With no further information on salinity and food conditions of culture in Egloff's study, I can claim only comparable results with respect to overall generation time.

Despite the relative consistency of egg hatching time, the determination of brood size and the potential mechanism for hatching are yet unclear. Provasoli et al. (1959) suggested that hatching in *T. californicus* and *T. japonicus* may be induced by light; Kahan et al. (1988) proposed the transmission of chemical messengers from the female in *T. japonicus*. The potential for differential egg viability or sex ratio from natural egg sac deposit relative to 'forced' hatching has not, to my knowledge, been studied. Egg sacs will usually hatch within 24 hours when deposited from live females. Sacs are dropped from sacrificed individuals almost immediately, with the eggs again hatching within 24 hours (Vacquier and Belser, 1965; Kahan et al, 1988). Egloff (1966) described a method for egg examination by dissolving the sac in a solution of 20 - 30% Chlorox bleach (sodium hypochlorite), but in practice, any solution applied to the sac will likely be carried to the eggs and may affect their viability; I have found that the brood sac is best removed from the gravid female using micro-forceps. To avoid damaging the egg sacs, Kahan et al. (1988) sacrificed adult female *T. japonicus* by mechanical injury to the head; these authors also describe a method for specimen preparation for scanning electron microscopy (SEM) analyses. Egloff's (1966) results for the time required for egg

hatching (2.4 to 8.2 days) are quite different from the current results, which may either be due to 1) the means of separating the egg sac; or 2) Egloff presenting his data as the total time from insemination, not the time of egg sac formation.

The duration of each N-stage is approximately one day, with the exception of the N-III and N-VI stages, which are of slightly longer duration. The current study used equal initial numbers of nauplii for both "winter" and "summer" cultures, however Lee and Hu (1981) achieved their highest mean number of *T. japonicus* nauplii (36) at a salinity of 30.7‰. Upon molting to copepodite stages, the duration for each stage increases to two to three days, and often three to four days at 10 - 15°C. From Table 5.1, the formation of an additional somite and the onset of an additional pair of swimming appendages is indicated for stages C-I to C-III, with sexual dimorphism occurring at the C-IV stage. The range of body lengths observed in the current study agrees generally with the sizes provided in Ward and Whipple (1959): 0.94 - 1.1 mm for males, 0.96 - 1.4 mm for females, although I find the C-VI males to most usually have a longer (and generally larger) prosome and urosome than the female. Longevity of the C-VI adults in culture has not been accurately established, but appears to depend principally on the quality of the support media, notably the amount of bacteria present and the avoidance of accumulated wastes. Adults isolated from my stock cultures have survived for more than 30 days, and Vittor (1971) estimates a lifespan of 100 to 140 days for *T. californicus* at 20°C.

Brood Size: The mean brood size obtained within either temperature range (20 ± 4.2 eggs at 10 - 15°C; 26 ± 8.1 eggs at 18 - 20°C) is considerably lower than results of Comita and Comita (1966), who derive a first brood average of 32 at 11 °C in *T. brevicornis*. Harris (1973) records a brood size of 27.5 eggs · clutch^{-1} at 10°C and 28.3 eggs · clutch^{-1} at 20°C for the same species, though a change in brood size with rearing temperature is not indicated. For *T. californicus*, the current results from culture approximate more closely mean value of 18 eggs · clutch^{-1} provided by Huizinga (1971)

and the median value of 20 eggs · clutch^{-1} reported by Vittor (1971, p. 40) for *T. californicus* in "100% sea water" at 20°C. While his observed brood sizes were also highly variable, Vittor's (1971) results do not indicate that brood size is enhanced with higher food abundance; increased energy reserves for reproduction may instead be invested in the production of a greater number of brood sacs. Egloff (1966) found *in situ* broods for *T. californicus* to range from 15 to 140 eggs with a mean of 46 and mode of 32, which again might be attributed to differences in food availability, or a difference in the brood sacs enumerated. Comita and Comita (1966) observe an increase in clutch size from the first through the third broods; while I removed the first observed egg sac from laboratory culture females, it could not be determined which brood was removed from gravid females sampled from pools.

Mating: Burton (1985) sufficiently summarized the mating system in *T. californicus*, and notes that males may clasp C-II to C-V females for up to a week before the female's terminal molt. Females are noted to mate only once, as there is no evidence of sperm displacement, while males were observed to inseminate an average of 2.5 ± 0.8 females in 72 hours (Burton, 1985). Given a lifespan of 50 to 80 days for the adult (also from Vittor, 1971), it is conceivable that some 300 progeny could be produced from a single insemination (calculations by Burton, 1985), which compares to the total of 301 eggs produced from a single *T. brevicornis* female, calculated by Harris (1973).

In many samples, *T. californicus* is seen to be almost entirely clasped into mating pairs. Clasping for a duration longer than is needed for sperm transfer is not uncommon in crustaceans (e.g., Manning, 1975; Shuster, 1981; Thornhill and Alcock, 1983), and Burton (1985) noted that, since clasping is done with the antennae, feeding may still occur in the male and the female while in the riding position. There may be a tremendous cost associated with long-term clasping, but the ability of males to mate several times, while the females mate only once, will produce a low frequency of available females and finding the most mature female will consequently reduce the amount of time invested in

mating. Mate guarding is frequently noted to occur in situations where there is a paucity of potential mates and is supported by observations of two or more males attempting to clasp a single female. The observation that males clasp 'females' as early as the C-II stage, suggests (though does not confirm) that male copepods can distinguish females before the sexually dimorphic C-IV stage. The cost to the male then becomes not the production of sperm, but the reproduction missed while remaining clasped to an unreceptive female until the C-V molt. It is also not known how often males may clasp mistakenly an immature copepodite that develops into another male or whether clasping affects the sex determination.

Bozic (1960) suggested that fertilization of the female must occur immediately after the terminal molt, but Egloff (1966) and Burton (1985) revise this, and observe that fertilization may occur any time after the terminal molt. Harris (1973) observed a delay of six days between the female molt from the C-V stage to the adult, and the onset of egg production in *T. brevicornis*. Given the above conditions, the availability of mature, unfertilized females is likely rare, and Burton (1985) noted that if fertilization occurs prior to the terminal molt, non-viable eggs are produced. My observations as well as those of M. Spaeth (pers comm.) suggest that the terminal, C-V to C-VI molt may not occur in *T. californicus* females *unless* fertilization occurs. This observation, as well as further clarification of the effect of differential temperature and salinity on body volume and the production of successive broods is here proposed as an avenue for future study.

CONCLUSIONS

Tigriopus californicus was observed to develop through the "typical" harpacticoid life-history of six naupliar and six copepodite stages, which somewhat revises and clarifies earlier descriptions, including that of Huizinga (1971). Development of nauplii (stages N-I through N-VI) occurred in 10 days under 'summer' conditions and 12 days under 'winter' conditions; copepodite development (stages C-I through C-VI) was similarly

delayed from 11 to 18 days at the lower temperature/salinity. Total generation time (egg to adult) was 21 days for the higher temperature/salinity values, and 30 days at the lower values, although no net difference in body length was observed. Clutch size was 20 ± 4.2 eggs (mean ± S.E.) at 10 - 15°C and 26 ± 8.1 eggs at 18 - 20°C. for gravid females in culture; field specimens had a mean clutch size of 23 ± 2.5 eggs at 10 - 15°C, increasing to 37 ± 4.2 eggs · clutch^{-1} during the summer months (July and August), and possibly indicative of the quality and supply of food available *in situ*. Non-viable progeny accounted for 10 ± 8.1% and 10.8 ±7.8% of all eggs under 'summer' and 'winter' conditions, respectively.

CHAPTER 5: SEASONAL ABUNDANCE AND POPULATION FLUX OF *TIGRIOPUS CALIFORNICUS* IN BARKLEY SOUND

INTRODUCTION

"Chaos often breeds life, when order breeds habit."

— HENRY ADAMS (1907)

Sampling considerations endemic to the study of oceanic or fresh water plankton populations are equally applicable to the study of microcrustacea in isolated coastal areas such as estuaries, salt marshes, seagrass beds and coastal pools. Such general considerations include: spatial heterogeneity (Barnes, 1949; Wiebe, 1970; Smith et al., 1976; Mackas et al., 1980; Beers et al., 1981), organism response and behavior (Forward and Cronin, 1980; Harris and Morgan, 1986; Lampert, 1989; Hough and Naylor, 1992; Haney, 1993; Lampert, 1993), atmospheric and hydrological effects (Brooks, 1979; Calaban and Makarewicz, 1982; Kimmerer and McKinnon, 1987), sampling scheme and sampler design (Beers et al., 1967; Omori and Hamner, 1983; reviewed in Powlik et al., 1991). A number of studies have utilized the natural abundance, small size, and comparatively short generation time of copepod populations within these smaller and discrete habitats to model or estimate processes for meiofaunal populations, including: distribution and migration, life-history strategies, feeding and excretion, production, growth, aging, and decay (Egloff, 1966; Vittor, 1971; Heip and Smol, 1976; Feller, 1980; Palmer, 1980; Thistle, 1980; Kimmerer and McKinnon, 1987; Paffenhöfer and Stearns, 1988; Kern, 1990; White and Roman, 1992; Dybdahl, 1994).

Egloff (1966) suggested that results on the population structure, age, sex ratio, and density-depended behaviors observed in splashpool copepoda may be extended in

application to pelagic plankton assemblages. However, the designation of true 'replicates' among littoral pools is made more difficult by localized differences in tidal elevation, exposure to wave wash, pool water properties, resident meiofauna, vegetation and shore debris (Metaxas and Scheibling, 1993). Moreover, the smaller, isolated volume of coastal pools enhances the effects of oxygen production, changes in pH, bacterial activity on detrital material or accumulation of chemical exudates, toxins or pollutants, and potentially noxious wastes. Even minor changes in any of these parameters may have a substantive effect on the entire volume of the pool, and the action of a single wave or storm event may potentially replenish or decimate the entire population of a pool (Vittor, 1971; Dethier, 1980, and the preceding chapters) Battaglia (1970) additionally cautioned that any models or population studies derived from such a specialized, highly variable habitat will not easily translate to speculation about less specialized or extreme habitats.

As isolated (or semi-isolated) vessels for mensurative or manipulative studies of aquatic ecology *in situ*, splashpools and fresh water rockpools are without comparison for their ease of access, demarcation of the water mass to be sampled, and provision of a stable work platform. These benefits are counter-balanced by other factors that comparatively affect smaller water masses to a much greater extent, including: heating by solar radiation, cooling by wind, evaporation, and dilution by precipitation (Morris and Taylor, 1983; Thiéry et al., 1995), eutrophication produced from stagnation, the deposit of debris, or nitrification from animal excreta (Ganning and Wulff, 1969), habitat complexity (Hicks, 1980; Coull and Wells, 1983), or the enhanced number and diversity of competing, grazing or predating organisms (Fraser, 1936; Barnes, 1949; Guberlet, 1956; Lubchenko, 1978; Kozloff, 1983: Lampert, 1993).

The descriptions of *Tigriopus* development in laboratory culture far exceed those studies addressing population density, growth, and extinction of field populations of splashpool copepods (see previous chapters). Population "maxima" are reported, usually only as individuals mL^{-1} or L^{-1}, with little further detail provided. As with most of

ecology, early studies of *Tigriopus* field populations (e.g., Igarashi, 1959, 1960) were primarily qualitative in their observation, or provided only anecdotal accounts of field conditions (but see Fraser, 1936 a, 1936b). Later studies sought to relate the response of *Tigriopus* populations - usually in the laboratory - to broader ecological paradigms of the day, including the expression of sex ratio (Vacquier and Belser, 1965; Egloff, 1966), population structure and strategy for growth (Vittor, 1971; Harris, 1973), or the influence of predation on intertidal distribution (Dethier, 1980). More recently, Dybdahl (1994, 1995) addresses the extinction of *T. californicus* populations as it pertains to founder effects and re-colonization, but bases his calculations on several inapplicable assumptions. A reliable, predictive estimate for the growth and decline of *Tigriopus* field populations has not been published.

The foregoing studies and discussion in this thesis have sought to provide parameters (or ranges of parameters) that are descriptive of the seasonal conditions found in the supralittoral splashpool of southeastern Barkley Sound. For the most part, these data were collected during short (one-to-two week) sampling intervals, providing a 'snapshot' of extant conditions throughout the year (Figure B1; Appendix C). However, given the ephemeral and highly variable physical and chemical conditions present in these pools, it would be instructive to determine how representative these observations are of the conditions experienced by *T. californicus* field populations for the remainder of the year.

The intent of the current chapter is to present data on the seasonal density and age structure of *T. californicus* populations in Barkley Sound, considering not only the nature of the habitat itself (Chapter 1), but more significantly, the processes occurring within inhabited pools, and even within the organism itself (Chapters 2, 3, and 4). Comparing the 'predicted' results for population florescence or extinction to conditions observed during the sampling intervals may then provide a measure of how representative or predictive these observations are for determining the dynamics of field populations.

Notes on sampling considerations for splashpools as well as the benefits and limitations of certain types of sampling gear will also be discussed.

MATERIALS AND METHODS

Field Sampling: Splashpools containing *Tigriopus californicus* were surveyed seasonally from field sites in southeastern Barkley Sound (see Chapter 1 for field site location and details of survey methods). For sampling copepods, each pool was divided into a numerically-assigned sextet, and a six-sided die was rolled to allow a randomized, triplicate sample. Copepods were then collected using a 30 mL graduated pipette drawn along the pool bottom at these randomly-assigned positions. Scouring, pumping, or more involved means of sampling the pools were avoided, as this may have produced an undesirable level of disturbance.

Pipette samples were stirred into a homogenous solution and split into two equal fractions: One fraction was narcotized *in situ* using 10% carbonated water (Gannon and Gannon, 1975) and enumerated to (approximate) life-history stage using a field microscope or jeweler's glass; the second fraction was returned to the laboratory, sacrificed, and identified to life-history stage under higher magnification (see Chapter 4).

In those pools where *T. californicus* was found, copepods were narcotized and counted in triplicate for: 1) male-to-female ratio; 2) ovigerous females, including 3) clutch size; 4) immature copepodites; and 5) nauplii present, averaged where repeated counts differed. Pools were considered lacking *T. californicus* if three successive pipettes contained no copepods.

In contrast to the usual sampling regime for the field sites (wherein each pool was sampled every two to three days during the sampling interval), pools selected for evaluating population density and flux were sampled each day for at least one week, or longer, depending on time availability. It was not possible in the time available to census all 85 tagged pools in this manner, hence a sub-sample of pools was selected by stratified random sampling from each field site in Figure 1.1 (see Results for n values used).

Estimating Population Size: The model provided here permits growth to the observed population maxima of 2,000 individuals · L^{-1} in winter and 20,000 individuals · L^{-1} in summer. From the assumed founding population of 10 individuals (Chapter 3), two individuals (20%) will be mature females, either carrying eggs, previously inseminated, or inseminated within 72 hours (assumed) of introduction; 3 will be mature males; and the remaining 5 individuals will be immature copepodites or nauplii, maturing in the first or second week following introduction. From Chapter 4, an average brood size of 23 eggs (winter) and 37 eggs (summer) is here assumed, with an average viability of 90%. Based on the results of the current chapter, I use a sex ratio of 1.46 (male:female) in winter and 1.36 in summer.

Maximum Population Size: I suggest that values of 2000 and 20,000 individuals · L^{-1} are representative of commonly observed maxima in winter and summer, respectively, however on at least one occasion I found natural concentrations of *T. californicus* in excess of 200,000 *adults* per liter, as calculated from a homogenous, 1/16-split sample (see Results). In application, these maxima will probably not be reached over the period of time estimates.

Population Growth: The generation time (egg to adult) of 30 days under winter temperatures and salinity, and 21 days under summer temperatures and salinity is assumed (Chapter 4). Other assumptions used in the calculation of Tables 5.3 and 5.4 are: 1) 10% mortality of nauplii molting to copepodites and a further 10 % mortality for copepodites molting from copepodites to mature adults; 2) a rate of development commensurate with the results of Chapter 5 at both summer and winter temperatures; 3) an adult longevity of at least 5 weeks; and 4) no population decimation due to biotic or abiotic factors.

Frequency of Extinction: For the current analysis, an 'extinction' was tallied each time a previously inhabited pool was found to be without *T. californicus* during subsequent sampling intervals; the reverse condition was taken to indicate 'colonization.'

Estimating Population Flux: The results and discussion of preceding chapters

provide the parameters of pool condition, seasonal population structure of *Tigriopus californicus*, and frequency of extinction or florescence. Where applicable, more pertinent (by season) or illustrative (by result) values from previous studies have been used (Table 3.1). For the purposes of estimating *T. californicus* population dynamics, the following assumptions will be applied to the 'model' of population growth and decline:

1. that the initial (founding) population is eight to 10 individuals, of various life-history stages, which is a 'typical' colonizing population from the results of Vittor (1971) and Dybdahl (1994). Following the results of Chapter 3, 50% of these colonizers will be mature adults (including gravid females), with copepodites and nauplii comprising the remaining 50% and maturing within one to two weeks;
2. that the male-to-female ratio initially approximates 1.47 in winter and 1.36 in summer (from the above results). The 'expected' ratio of 1:1 is rarely observed in natural populations (due to differential growth, mortality, or gender-specific selection by environmental conditions), and will vary according to season and rearing conditions;
3. that clutch size, time of hatching, and life-history stage development occurs at the same rate as observed in laboratory culture (Chapter 4) and is therefore estimated principally from seasonal temperature and salinity. While food type and quantity are also an essential consideration, this has not been included in the current calculations. Data on the specific food type and abundance available to splashpools in Barkley Sound was not collected for the current study, and a suitable description of *in situ* food resources for alternate, comparable field sites could not be located in the literature;
4. that mortality is based solely on the longevity of the organism itself. The influence of dispersal agents, competition, or predation have not been included in the calculations; and

5. that the pool volume may increase from precipitation and evaporate according to average climatic conditions (Chapter 3; Appendix B), but remains isolated from wave action. Further, that the dilution or evaporation imposed no deleterious effects.

The instantaneous rate of growth, birth, and death for *T. californicus* populations was calculated using the formulae of Paloheimo (1974) and Feller (1980). Using the exponential growth equation:

$$N_t = N_{to}e^{rt} \qquad (1)$$

r is the instantaneous rate of increase, N is the initial abundance of *T. californicus* (values for Day 1 in Tables 5.3 and 5.4, from a founding population of 10 individuals), and t is the elapsed time, in days.

Instantaneous birth rate (*b*) was then calculated as:

$$b = \ln(E+1)/D \qquad (2)$$

where E is the abundance of eggs (here estimated from clutch sizes under winter and summer conditions, per Chapter 4), and D is the time of development for the eggs (assumed to be 4 days for *T. californicus*, from the calculations of Vittor, 1971).

From Feller (1980) instantaneous death rate (d) was then calculated as:

$$d = b - r \qquad (3)$$

to derive the values of Table 5.5. Finally, the estimated rate of increase (*r*) was compared to the observed *r* for 3 pools on Helby Island in the summer of 1995, as illustrated in Figure 5.1. From Paloheimo (1974, cited by Feller, 1980, p. 463) these calculations assume a stable age distribution, constant birth and death rates, and fixed egg development. Feller (1980) suggests such assumptions, though applicable over short intervals (*ca.* 1 week), may not apply over longer intervals. Hence, the comparison illustrated in Figure 5.1 was only plotted for one week of observation.

RESULTS

T. californicus *Abundance:* Seasonal *T. californicus* abundance is summarized in Table 5.1. Total density remained remarkably consistent over the year, with the exception of winter, when it declined to 217 ± 401.7 individuals · L^{-1} from a seasonal means of 757 ± 2014.5, 835 ± 1750.6, and 644 ± 2220.2 individuals · L^{-1} in spring, summer, and autumn, respectively (means rounded to the nearest whole individual). Winter populations were also more sporadic in occurrence, concentrated into one-half to one-third of the pools normally occupied in other seasons. With enhanced evaporation and sustained isolation from replenishment in the summer months, I observed population densities of up to 200,000 individuals · L^{-1}; the highest value for the current data set was 21,456 ± 1750.6 individuals · L^{-1}, and similar 'maxima' were found in autumn, spring, and summer (Table 5.1).

The adult male-to-female ratio remained consistent at 1.36 in spring and summer, increasing to 1.84 in autumn and 1.47 in winter, with several dense populations occurring in coupled (riding) pairs to a significant extent. At the highest densities, samples were comprised virtually entirely of *T. californicus*, predominately of mature individuals, and with more than 80% of the females carrying egg sacs. Clutch size ranged from 23 ± 6.5 eggs · $female^{-1}$ in winter to 37 ± 10.2 eggs · $female^{-1}$ in summer.

Pool Duration: From the 14-year average precipitation for the area (Table B.1), a pool of typical size of 7.01 m^2 in winter and 3.38 m^2 in summer (Table 1.2) , would receive 6.8 x 10^{-2} L · day^{-1} and 8.9 x 10^{-3} L · day^{-1} in precipitation. Correcting for the average rates of evaporation recorded in Chapter 3, an average-sized *T. californicus* pool would evaporate in 8 to 9 days in winter or 4 to 5 days in summer, assuming it is not replenished by wave action. These and other parameters are summarized in Table 5.2.

Population Growth: Tables 5.3 and 5.4 summarize the calculations of total abundance from a hypothetical founding population of 10 individuals apportioned into the

life-history stages derived in Chapter 3. Figure 5.1 summarizes a comparison between daily measurements of *T. californicus* density from 3 randomly-selected Helby Island pools and the expected rates of growth, birth and death, using equations 1 - 3 and the model assumptions noted above.

Population Extinction: For the current analysis, an 'extinction' was tallied each time a previously inhabited pool was found to be without *T. californicus* during subsequent sampling intervals; the reverse condition was taken to indicate 'colonization.' Overall, 12 pools were found to contain *T. californicus* during every sampling interval, 12 of the randomly-selected pools were never observed to contain *T. californicus*, and the remaining 61 pools had intermittent or sporadic habitation. Among the five field sites, pools on Diana Island and Wizard Islet experienced the highest frequency of extinction at 48 ± 18% and 33.5 ± 16.6%, respectively (mean ± S.E.). The lowest frequencies of extinction were observed at First Beach (26.5 ± 15.2%) and Second Beach (29.8 ± 7.2%, see Figure 5.2).

TABLE 5.1. Seasonal *Tigriopus californicus* abundance, differentiated by generalized life-history stage. Tabulated mean values have been rounded to the nearest whole individual.

Individuals/L *Inclusive of stages:*	Nauplii (N-I to N-VI)	Copepodites (C-I to C-III)	Males (C-IV to C-VI)	Females (C-IV to C-VI)	Gravid Females (C-IV to C-VI)	Clutch Size (eggs)	TOTAL[a]
Autumn *							
mean	6	69	289	157	123	29	644
range	(0 -100)	(0 - 1250)	(0 - 11,680)	(0 - 2160)	(0 - 6320)	(2 - 43)	(40 - 20,600)
s.e.	17.5	151.5	1248.7	293.4	693.9	4.9	2220.2
n	88	88	88	88	88	20	88
Winter **							
mean	36	23	62	42	51	23	217
range	(0 - 580)	(0 - 300)	(0 - 500)	(0 - 275)	(0 - 900)	(6 - 29)	(8 - 2440)
s.e.	117.1	52.4	101.0	61.5	139.7	3.4	401.7
n	47	47	47	47	47	12	47
Spring ***							
mean	26	121	280	207	123	31	757
range	(0 - 886)	(0 - 5000)	(0 - 11,722)	(0 - 4600)	(0 - 6528)	(8 - 34)	(10 - 19,182)
s.e.	85.4	409.4	757.5	421.2	443.7	3.7	2014.5
n	384	384	384	384	384	75	384
Summer ***							
mean	31	115	318	235	136	33	835
range	(0 - 89)	(0 - 5218)	(0 - 11,244)	(0 - 4350)	(0 - 6118)	(22 - 39)	(17 - 21,456)
s.e.	89.7	381.7	728.8	422.2	438.1	2.8	1750.6
n	448	448	448	448	448	38	448

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

[a] = total individuals L^{-1}, excluding unhatched eggs.

TABLE 5.2. Parameters used for the calculation of *in situ* population growth and decline of *Tigriopus californicus*. Except where specified, values used were derived in the current study. Standard error (mean ± S.E.) or observed range (minimum - maximum) for values are provided where applicable; mean values are used for the calculation of Table 5.3.

Factor	Parameter (units)	Winter Value (January)	Summer Value (July + August)
Basin	Volume (L)	8.9 ± 17	5.2 ± 67
	Surface Area (m^2)	7.01 ± 12.5	3.38 ± 6.7
	Water Temperature (°C)	10.7 (7 - 14)	21.8 (17 - 33)
	Salinity (‰)	21.4 ± 9.1	40.1± 17.2
	Precipitation (mm /day)	10.8 ± 5.5	2.6 ± 2.49
	(L / day)*	6.8×10^{-2}	8.9×10^{-3}
	Volumetric Flux (L / day)	1.10	1.47
	Pool Duration (days)	8 - 9	3 - 4
Population	Founding Population	3 male 1 female w/ clutch 1 female 5 nauplii + copepodites	3 male 1 female w/ clutch 1 female 5 nauplii + copepodites
	Initial Count	10 + clutch	10 + clutch
	n	28	28
	Sex Ratio (Male:Female)	1.47	1.36
Individuals	Clutch size (# eggs)	23 ± 6.5	37 ± 10.2
	Egg mortality (%)	10.8 ± 7.8	10 ± 9.1
	Duration as Nauplius (days)	12	10
	Duration as Copepodite (days)	18	11
	Generation Time (days)	30	21
	Duration as Adult (days)	35	35
	Natural Survival (%)	90	90
	Potential Mates (males)	3	3
	Potential Broods (females)	3	3

* Average daily preciptation in millimeters over the pool surface area indicated.

TABLE 5.3. One week abundance and age structure predicted for *Tigriopus californicus* founding populations. Assumptions: a founding population of 10 individuals plus average clutch sizes of 23 (winter) and 37 (summer) from Chapter 4; 10% mortality at hatching and nauplius/copepodite and copepodite/adult transitions; growth rate per Chapter 4 and an adult longevity of 5 weeks. No predation or decimation due to wave action is included in the calculation. Density is tabulated as individuals $\cdot L^{-1}$.

Time After Founding	Life-History Stage	Winter (January)	Summer (July + August)
1 Day	Males	3	3
	Females	2	2
	Copepodites	3	3
	Nauplii	2	2
	Eggs	23	37
	TOTAL	33	47
2 Days	Males	3	3
	Females	2	2
	Copepodites	3	3
	Nauplii	23	35
	Eggs	0	0
	TOTAL	31	43
3 Days	Males	3	3
	Females	2	3
	Copepodites	3	2
	Nauplii	23	35
	Eggs	0	0
	TOTAL	31	43
4 Days	Males	3	4
	Females	3	3
	Copepodites	3	3
	Nauplii	22	33
	Eggs	0	0
	TOTAL	31	43
5 Days	Males	4	4
	Females	2	3
	Copepodites	2	3
	Nauplii	22	33
	Eggs	0	0
	TOTAL	31	43
6 Days	Males	4	4
	Females	3	3
	Copepodites	2	3
	Nauplii	22	33
	Eggs	46	74
	TOTAL	77	117
1 Week	Males	5	6
	Females	4	5
	Copepodites	1	39
	Nauplii	63	126
	Eggs	0	0
	TOTAL	73	176

TABLE 5.4. Five week abundance and age structure predicted for *Tigriopus californicus* founding populations. Assumptions per Table 5.3, with the proportion of life-history stages at one week equal to the results of Table 5.3. Density is tabulated as individuals · L^{-1}.

Time After Founding	Life-History Stage	Winter (January)	Summer (July + August)
1 Week	Males	5	6
	Females	4	5
	Copepodites	1	39
	Nauplii	63	126
	Eggs	0	0
	TOTAL	73	176
2 Weeks	Males	5	16
	Females	5	13
	Copepodites	30	20
	Nauplii	31	63
	Eggs	41	100
	TOTAL	112	212
3 Weeks	Males	23	27
	Females	14	21
	Copepodites	27	57
	Nauplii	37	90
	Eggs	62	233
	TOTAL	163	428
4 Weeks	Males	36	67
	Females	25	42
	Copepodites	33	81
	Nauplii	56	210
	Eggs	228	533
	TOTAL	378	933
5 Weeks	Males	49	100
	Females	33	72
	Copepodites	50	189
	Nauplii	205	480
	Eggs	414	1132
	TOTAL	751	1973

TABLE 5.5. Instantaneous growth, birth, and death rates for founding populations. Mean abundance (total individuals · L^{-1}, based on a founding population of 10 individuals) and clutch size per Tables 5.3 and 5.4 under winter and summer conditions (see Chapter 4). All calculations use time (t) in days; from Vittor (1971), an egg development time of 4 days is assumed. See text for other assumptions and formulae.

Time (days)	Season/Conditions (per Chapter 5)	Instantaneous rate of increase (*r*)	Instantaneous birth rate (*b*)	Instantaneous death rate (*d*)
1	Winter	- 0.063	0.795	0.858
	Summer	- 0.089	0.909	0.998
2	Winter	- 0.031	0.000	0.037
	Summer	- 0.044	0.000	0.044
3	Winter	- 0.021	0.000	0.021
	Summer	- 0.030	0.000	0.030
4	Winter	- 0.014	0.000	0.014
	Summer	- 0.022	0.000	0.022
5	Winter	0.169	0.960	0.791
	Summer	0.182	1.079	0.897
6	Winter	0.132	0.000	- 0.132
	Summer	0.152	0.000	- 0.152
7	Winter	0.113	0.000	- 0.113
	Summer	0.130	0.000	- 0.130
14	Winter	0.087	0.930	0.006
	Summer	0.108	1.177	1.069
21	Winter	0.076	1.036	0.960
	Summer	0.105	1.364	1.259
28	Winter	0.087	1.360	1.271
	Summer	0.107	1.570	1.463
35	Winter	0.089	1.507	1.418
	Summer	0.107	1.758	1.651

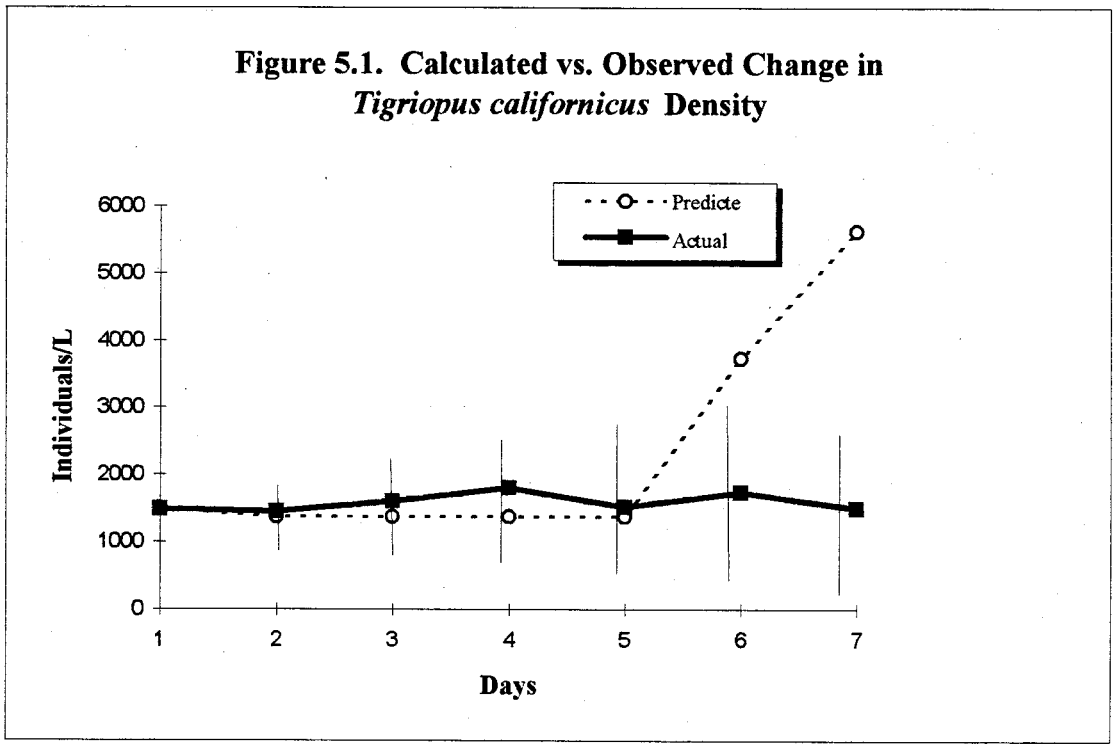

FIGURE 5.1. Calculated versus observed change in *Tigriopus californicus* density. Using summertime data, the scored line indicates the predicted change in density from Tables 5.3 and 5.4. Solid line represents the observed abundance, as calculated from daily samples from 3 Helby Island pools. Discrepancies exist due to avoidance of the sampler, and the assumptions of the model (see text). Increases in predicted density (per the calculations of Table 5.3 and 5.4) derive principally from the production and hatching of broods.

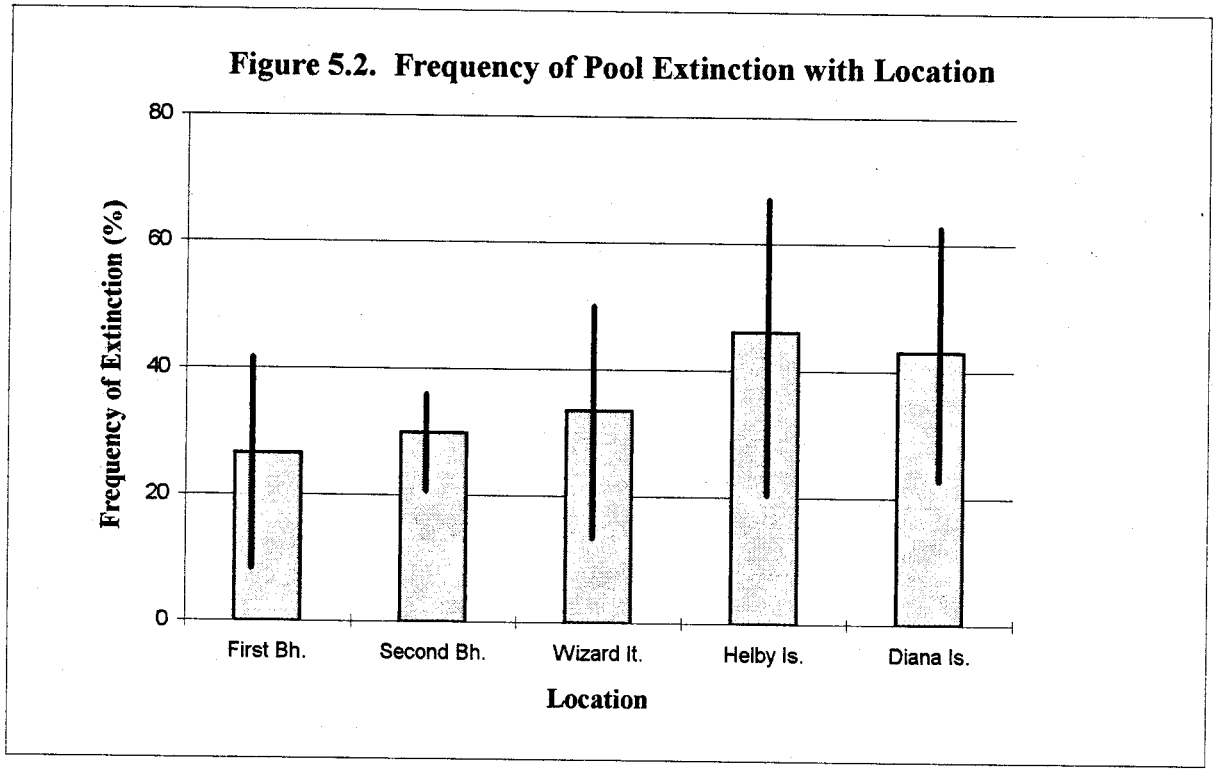

FIGURE 5.2. Frequency of copepod extinction with location. Average frequency of *Tigriopus californicus* population extinction for all pools at each field location. For data presentation, an 'extinction' event was tallied when a previously inhabited pool was found to have no copepods during a subsequent sampling interval. Values presented as mean ± S.E.

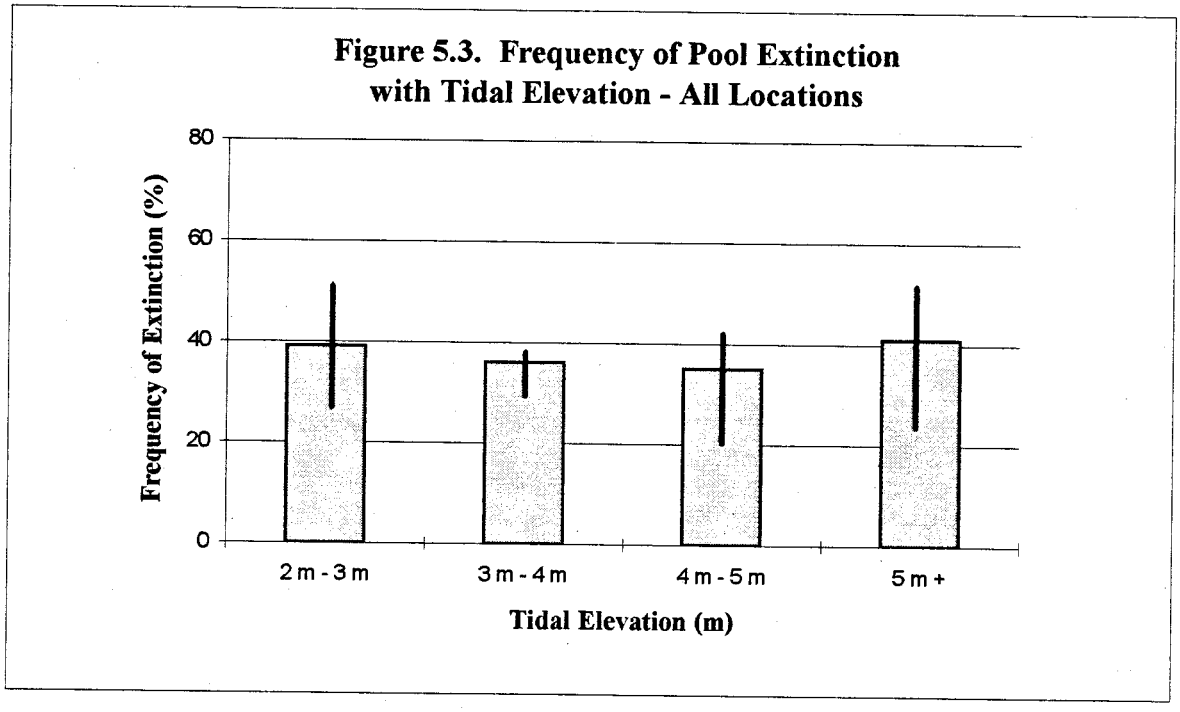

FIGURE 5.3. Frequency of copepod extinction with tidal elevation. Average frequency of *Tigriopus californicus* population extinction with shoreline elevation for all pools. For data presentation, an 'extinction' event was tallied when a previously inhabited pool was found to have no copepods during a subsequent sampling interval. Values presented as mean ± S.E.

DISCUSSION

Sampling Considerations

Sampling Considerations: Perhaps the three most significant obstacles to estimating the microcrustacea populations *in situ* are: 1) accurate and representative sampling of the organism at all life-history stages; 2) an accurate determination of birth rate; and 3) an estimate of the natural longevity of each age-class, including possible sources of mortality on juveniles as well as adults. In the first instance, at least a cursory understanding of the organism's natural history is required for the selection of appropriate sampling gear (sample volume, mesh size, number or replicates). For the derivation of birth and death rates, clutch size, egg viability, time of first hatching, and larval survival can (and often are) estimated from organisms in culture under a variety of conditions, however the conditions under which an organism 'thrives' may have little or no resemblance to the natural conditions of the organism's habitat.

While *T. californicus* populations occur largely within the relatively small, discrete volumes of supralittoral splashpools, representative sampling of the organism at all life-history stages cannot be assumed. The organism exhibits a dive-and-cling swimming behavior (Egloff, 1966; Vittor, 1971), and an escape response that appears to be stimulated by shadows or microscale changes in hydrostatic pressure. Measures can be taken to prevent undue disturbance of the pools and thus the escape of individuals (particularly adults) from the sampler, however the nauplii and egg stages, which have less-developed swimming ability, are found in association with the phytobenthos on the bottom of pools and are often much more difficult to collect.

The shallow depth of most splashpools precludes the use of more traditional sieves, nets or pumps, which cannot be properly submerged or maneuvered. Burton and Feldman (1981) collected *T. californicus* by scooping pools directly into plastic bottles or using a fine mesh for low-density populations; the method most commonly described for

culture specimen collection. Harris (1973) drew 100 mL samples using a 63 μm sieve, a procedure which may not capture all life-history stages of *T. californicus*. Fraser (1936a) and Monk (1941) sampled pools by siphoning water through a net or bailing the pool of all its water, a procedure which may be disruptive for some applications. Dethier (1980) estimates population numbers from the number of individuals passing over a miniature Secchi disk, but this method permits enumeration only, without specimen identification to any appreciable degree.

I have used, alternately, a calibrated 30-mL pipette or scoops of a 12 cm diameter (400 mL) glass preparation dish for sampling splashpools. The wider catchment area and transparency of the glass reduces the pressure wave and visual cues produced by the sampler, at the expense of sampling close to the substratum. This latter consideration is not incidental, as the majority of a population - especially nauplii - may subsist near the bottom of the pool and may be under-sampled unless consideration is given to the surface irregularities of the pool basin. The use of a large, calibrated pipette (or turkey baster) is preferred for drawing a smaller volume of the pool, yielding a discrete, high velocity sample of the substratum which does not damage nauplii or egg sacs, and sample processing time is reduced. Irregular topography and calculations from averaged dimensions can produce a high degree of error, and siphoning all the water from a pool may be the only means to determine pool volume accurately. However, such a degree of disturbance to the ecosystem in order to measure a parameter noted to experience daily or even hourly flux should also be considered.

Escape response should be considered as a source of error principally in the collection of adult specimens, since eggs and nauplii prior to the N-III stage do not exhibit directed swimming behavior (Chapter 4). Both Egloff (1966) and Vittor (1971) described a 'dive and cling' swimming response of *T. californicus* to water agitation. The magnitude of this response will depend on the size of the disturbance produced by sampling, and so care should be taken: 1) to avoid casting shadows; and 2) to avoid

undue agitation of the water prior to collection; Egloff (1966) used a 0.5 liter bowl and sampling at dusk to compare possible temporal variation. During several nighttime collections (unpublished data), a flashlight beam trained directly on a swarm of *Tigriopus* in the water column of their pool produced neither a positive nor a negative phototaxis, possibly indicating that the intensity of the light was not sufficient to elicit phototaxis. Moreover, although *T. californicus* exhibit this quick-start potential, all stages appear to fatigue quickly and soon settle out when placed in deeper volumes of water. It was not determined whether the organism may respond similarly to changes in pressure or light from the non-visible spectra.

Mature (copepodite and adult) *T. californicus* are observed to utilize the full extent of the 'water column' available in their shallow pools, with dense populations often coloring the water orange with 'clouds' or 'swarms' of swimming individuals. Hicks and Coull (1983) and Bell et al. (1988) found mature female copepods to also favor the substratum, while males and immature females may utilize the water to enhance the opportunity for pre-copulatory encounters. Feeding of all life-history stages occurs along the substratum as the organism browses surfaces for adsorbed bacteria or microalgae, however this does not preclude incidental filtering of materials in solution (Harris, 1973), or the uptake of dissolved organic material (DOM) across the cuticle (Khalov and Yerokhin, 1971; Carli et al., 1993).

Given the heterogeneity or patchiness of *T. californicus* populations, a random or stratified-random method for selecting sample locations is the most desirable. Within pools, patches or aggregations of microbes do not generally predict patches of meiofaunal consumers (Dauer et al., 1982; Montagna et al., 1983), and the results of the current thesis (Chapter 2) do not suggest higher densities of *T. californicus* in association with either macroalgae or the higher concentrations of organic matter associated with vegetation. Although temporary stratification of splashpools may occur under static conditions (Morris and Taylor, 1983), this condition is easily disrupted by wind or wave

action, and it could not be determined if the organism associates with microscale thermoclines or haloclines within pools[1].

While the dried algal material used for the experiments of Chapter 3 contained ostensibly higher accumulations of *T. californicus*, this observation is the result of populations being compacted and stranded in a comparatively restricted area due to evaporation of the pool. For this same reason, density of field populations is better presented as individuals per unit pool volume, rather than per unit of the volume sampled; samples recorded only as individuals mL^{-1} or L^{-1} may erroneously suggest a bloom or decline in copepod abundance, when what is actually indicated is evaporation or dilution of the pool itself. Since pool volume can change over as little as a few hours, the method of Chapter 1 (estimating pool volume from averaged dimensions) should suit most applications. Even pumping all the water from a given pool (to derive an accurate estimate of pool volume), may not sufficiently collect all individuals from crevices in the incised bedrock and may even reduce estimates from those obtained from pools sampled while filled.

Seasonal Abundance and Density of *T. californicus*

In Fraser's (1936a) examination of the supralittoral zone, plankton densities were found to be three to 40 times more dense than littoral collections, and comprised of only two species, compared to 12 species found lower in the littoral zone. Overall, the present calculations of population density agree with previously published values for *in situ* conditions (e.g., Harris, 1973; Dethier, 1980). In Barkley Sound, *T. californicus* appears to reproduce throughout the year, establishing population density maxima of approximately 20 individuals $\cdot$ mL^{-1} in autumn, spring, and summer. Winter populations are not only reduced in density by as much as two-thirds (Table 5.1), but are also found in fewer pools, with *T. californicus* persisting, but retaining 'foxholes' in a smaller number of

[1] This would be doubtful, given the organism's demonstrated tolerance to temperature, salinity and pressure under laboratory conditions.

habitable reservoirs. Proportions of the life-history stages were also consistent in these three seasons, while the representation of nauplii in all seasons was much lower (overall average = 28 ± 7.4 individuals· L^{-1}) relative to copepodite and adult abundance than would be expected, for example, in pelagic copepod assemblages (but see Dybdahl, 1989).

Burton and Feldman (1981) suggested that, while complete extinction of *Tigriopus* populations is unlikely, regular depletion of populations may occur, either due to wave activity or seasonal changes in climate and water properties. Dybdahl (1994) considered *T. californicus* pools on the same rock outcrop as forming a metapopulation: a collection of local populations experiencing periodic extinction and re-colonization, which is especially characteristic of subdivided or fragmented habitats. He further reported extinction of *T. californicus* populations in 35% of his study pools over a period of six to eight weeks. On occasion, I have discovered pools of *T. californicus* which were nearly all apparently deceased. Temperature and salinity were not anomalous in these pools, 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 (Chapter 3).

In Barkley Sound, *T. californicus* does not appear to exhibit a bloom in numbers during any season. Although populations may become concentrated into a smaller volume by evaporation, this is not the same as an increase in absolute number. For this reason, copepod density is more correctly recorded as individuals · L^{-1} per unit pool volume. Upon finding a splashpool habitable, *T. californicus* appears to increase rapidly in density and remain there until the population is decimated, or spread to another water deposit, which agrees with the findings of Vittor (1971).

Egloff (1966) suggested that summer populations of *Tigriopus californicus* are influenced less by storm activity and wave splash. While wave conditions may be less

extreme in the summer, I suggest the influence of evaporation and stagnation may become much more pronounced, particularly in warmer climates. Further, 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 re-hydration (Chapter 3). Hence, in comparing the conditions of *Tigriopus*-inhabited pools, parity of season and latitude between study sites are essential considerations.

The male-to-female ratio for the current study averaged 1.41 ± 0.23 for the entire year, which compares with the findings of Egloff (1966) and Vittor (1971). Adults frequently occur almost entirely in clasped (though not necessarily mating) pairs, at times with multiple males competing for a single female. Smaller females are also sometimes difficult to differentiate from copepodites, and this is a potential source of error in population counts. Evaporation has the effect of concentrating those individuals retained in pools, and will undoubtedly influence oxygen consumption, food resource utilization, and mating behavior among splashpool copepods. At high densities (i.e., those in excess of 20 individuals $\cdot$ mL^{-1}), density-dependent behaviors such as inhibition of egg deposition (Kahan et al., 1988) or maternal cannibalism on nauplii (Lazzaretto and Salvato, 1992), a biasing effect on one or the other gender has not been demonstrated.

Estimating Changes in Population

Population Growth and Longevity: In order for birth rate to be determined, the: 1) egg number; 2) age at first reproduction; 3) rate of brood production; and 4) sex ratio must be known. Published accounts of population growth for *Tigriopus* copepods have been less than satisfactory (but see Harris, 1973). Morris et al. (1980, p. 632) claimed *T. californicus* populations "can double every 6.6 days at 15°C and every 3.9 days at 23 °C," but this claim is unremarkable unless the gender and age structure of the initial population is specified. Dethier (1980) calculated a population gain of 13 copepods $\cdot$ L^{-1}

· day $^{-1}$, but while this study compared experimental and control pools of equivalent volumes, no mention is made of physical conditions.

Vittor (1971) reported a generation time of 32 days at 15°C and 18 days at 25°C, with a total lifespan time of 130 ± 14 days at 15°C and 80 days at 25°C for *T. californicus*; Harris (1973) reported a longevity of 55 days at 15°C for *T. brevicornis*, and Ito (1970) a longevity of 70 days for *T. japonicus*, values that are undoubtedly linked to rearing conditions beyond temperature alone. Between the sexes, Egloff (1966) found female *T. californicus* to be longer lived (by 1.9 times) than males, with this effect enhanced at lower temperatures. Under starvation conditions, females were observed to live 3.7 times as long as males, again at lower temperatures[1].

From Table 4.1, the egg-to-adult generation time is more than a week longer under "winter" temperatures and salinity, requiring 30 days for the complete development of the organism, compared to 21 days under "summer" conditions. Such a delay could be considered disadvantageous during the winter ~~*in situ*~~, when storm activity, wave action on the shore, and hence the potential for wash-out of pool populations may be enhanced. Igarashi (1959) noted an inverse correlation between the frequency of pool flushing and the age and stability of *Tigriopus* populations; the effect of wash-out would be magnified on younger life-history stages (pre-N-III stage), which have less developed swimming ability (Chapter 4). Conversely, the comparatively more rapid development of *T. californicus* under "summer" conditions might be considered advantageous, since summertime pools are generally more prone to evaporation.

Population Density: Egloff (1966) used triplicate samples of 6 pools to determine the absolute size of a *T. californicus* population. His samples ranged from 242 to 1938 individuals · L^{-1}; conservative estimates, he cautions, due to the organism's avoidance of sampling gear. Interestingly, however, this in situ 'maxima' closely approximates the five

[1] This enhanced longevity may be explained by higher levels of polyunsaturated fats in the female, which may provide nutrition in the absence of food.

week total for summer populations calculated here (1973 individuals · L^{-1}, Table 5.4). Dethier (1980) reported *in situ T. californicus* densities as high as 2333 individuals L^{-1} (recorded as 35 individuals · 15 mL^{-1}) for spring samples, but did not differentiate these to life-history stage. The same could be said of most studies, which either omit the size of the basin (pool volume), the life-history stage, or all life-history stages in the reporting of population density.

Fecundity and Sex Ratio: Published accounts of sex ratio for *Tigriopus* copepods are typically varied. Belser (1959) provided a figure of nearly 4.0 (75 to 80% males) in *Tigriopus* populations (season and species not stated), while Egloff (1966) found a range of 1.07 to 5.0 (7 - 84% males) in his field populations. Lazzaretto et al. (in press, cited in 1990) note a ratio of 1:1 for *T. fulvus*, which is contrary to the observations of most natural populations. Factors contributing to fluctuations in sex ratio or life-history traits are evaluated extensively in the theses of Egloff (1966) and Vittor (1971), respectively. Differential life span, population density, time of year and longevity of the pool are all responsible for the observed sex ratios of field populations (see Table 5.2), however sex ratios approximating 1:1 may occur in very dense populations, where nearly the entire population may be conjoined in mating pairs (Chapter 4).

In populations growing slowly, the percentage of males (which typically mature more quickly than females) would be expected to increase (Egloff, 1966), which at least in part explains the decline of sex ratio in the current study from 1.46 in winter to 1.36 in summer. Conversely, sex ratio decreases in rapidly growing populations, or those moving into increasingly stressful conditions as more females are produced (Egloff, 1966), however the absolute density of females in a population may be more significant than the density of females relative to males. Although newly-established populations of low density, as in recently colonized pools, would benefit from a decreased sex ratio (i.e., having more females), this potential for population growth may not be realized, as the

increased production of nauplii may be curtailed by increased instances of maternal cannibalism (Egloff, 1966). Egloff (1966) also found no correlation between sex ratio and population density, however more females were produced under cooler, more saline or darker conditions. He concluded that either 1) males are less resistant to stressful conditions; or 2) male-to-female conversion is encouraged by stress (*cf.* Vacquier, 1962; Vacquier and Belser, 1965 for response to hydrostatic pressure). The increased production of males at higher temperatures reported by Egloff (1966) was not found in the results of Vittor (1971).

While insemination (and thus egg sac production) may continue to occur even at extremely high population densities, egg deposition appears to be inhibited, as indicated by the disproportionate abundance of gravid females (and mature life-history stages in general) in dense populations; it is not known for how long the eggs can be carried while still maintaining their viability. In general, unstable conditions and increased temperature will foreshorten generation time, including the time required for egg hatching (reviewed in Webb and Parsons, 1988). From studies of brood production in *Tigriopus* copepods (Comita and Comita, 1966; Harris, 1973; Chapter 5), egg size, viability, and clutch size are highly variable, but are apparently independent of rearing conditions. Many crustacea are poikilosmotic, and during high salinity flux, energy may be shifted from reproduction to osmoregulation. Vittor (1971) noted that *T. californicus* females are most fecund at 150% sea water, however Lee and Hu (1981) found the highest fecundity of *T. japonicus* to occur at 27.1‰ to 34.3‰ (approximately 100% sea water), though this comparison ignores the potential influences of food availability and other rearing conditions. Within some hypersaline pools, increased fecundity may be inconsequential: Dybdahl (1995) not only finds higher desiccation and osmotic stress in *T. californicus* pools on exposed shores (relative to sheltered locations), but also finds the proportion of females and juveniles to be lower in these populations and suggests a higher mortality of these life-history stages. In their review of harpacticoid copepods, Hicks and Coull (1983) tabulate

(from Huizinga, 1971): 3 broods · copulation^{-1} and 18 eggs · clutch^{-1} for *T. californicus*, which they consider low to average fecundity when compared to other species.

Fluctuation in T. californicus *Populations:* Burton and Feldman (1981) suggested that, while complete extinction of *Tigriopus* populations is unlikely, regular depletion of populations may occur, either due to wave activity or seasonal changes in climate and water properties. Using a vital stain, R. Burnett (pers. comm,, cited in Morris et al., 1980 p. 632) observed that the majority of individuals in *T. californicus* pools may 'overturn' within a few days, although the total density of the population remains similar. Dybdahl (1994) reported extinction of *T. californicus* populations in 35% of his study pools over a period of six to eight weeks, however these calculations do not consider the implications presented in the current study, of desiccation-resistant life-history stages (Chapter 3) or removal by dispersal agents (Chapter 1). From the current results, the "prediction" of population extinction is virtually impossible without further addressing such factors as swimming behavior of *T. californicus* under dynamic conditions and quantification of the effects of pool wash-out at the organismal level..

Splashpools on Diana Island and Wizard Islet experienced the highest frequency of extinction (48 ± 18% and 33.5 ± 16.6%, respectively) and the lowest frequencies of extinction were observed at First Beach (26.5 ± 15.2%) and Second Beach (29.8 ± 7.2%. While this may suggest that exposure to breaking waves increases the frequency of population extinction, such a conclusion is not supported by Figure 5.4, since the highest frequency of wave-produced extinction would be expected at or slightly above the mean water level (see Figure 1.2). Given the ephemeral nature of pool conditions and the sometimes lengthy intervals between sampling, any conclusions of sustained exclusion or inclusion of *T. californicus* also cannot be supported by these observations.

Based on the above calculations and comparisons to field populations, the predictive ability of calculated growth rates is also probably quite limited, even when applied to homogenous patches (inhabited pools) within a larger, heterogenous

distribution (patchiness among pools on a given shoreline). However, as noted in the preceding chapters, *T. californicus* populations appear able to increase their numbers to levels in excess of 20,000 individuals · L^{-1} throughout the year, regardless of pool size, tidal elevation, the percent-cover of macrofauna, or initial population number. While populations may be decimated by sudden changes in the habitat (e.g., heavy runoff, wave splash, pollutants), the organism possesses an innate ability to bloom from a very small population of varied life-history stages, to *in situ* densities that are without equal in coastal or offshore assemblages of microcrustacea.

CONCLUSIONS

Assuming that the sampling methods used provide representative samples of the abundance and age structure of splashpool populations, calculations of *T. californicus* growth based on *in vivo* measurements and observations appear to provide a reliable estimation only a portion of the time. Further, pools for which the assumptions of these calculations may be applied, namely those pools: 1) high enough to reduce the influence of dilution by wave splash and runoff; 2) small enough to deter colonization by potential predators or competitors; yet 3) large enough to resist complete evaporation are probably the exception to the norm and are not representative of the vast majority of the local populations in Barkley Sound. Ironically, pools that meet all these requirements to be suitable vessels for the study of "natural" populations virtually represent open air culture flasks, with less stringent control on abiotic variables such as water condition. For those pools not meeting the above criteria, I suggest that small volume pools (less than about 25 L) may be limited most significantly by evaporative processes or occasional wave splash; larger pools may persist under stratified conditions, but food availability may not be sufficient to support large copepod populations, especially where vegetation or sediment is scarce.

Regardless of pool volume or water conditions, *T. californicus* populations appear able to increase abundance to some *in situ* maximum, with the carrying capacity of any given pool, in the absence of stochastic events, probably dictated solely by the abundance of suitable food resources. At the highest population densities, egg hatching is apparently inhibited and the number of individuals remains at an elevated and consistent level. Complete 'crashes' of populations under stable conditions is probably unlikely, however thermal or haline shock, or displacement of individuals by wave splash, is undoubtedly a regular occurrence. As discussed in previous chapters of this thesis and studies such as Vittor (1971) and Dybdahl (1994), only a small number of dispersed individuals is likely required to colonize new pools, provided pool conditions remain habitable.

GENERAL DISCUSSION

The preceding observations have sought to extend the understanding of various aspects of the ecology of *Tigriopus californicus* that have either not previously been described or have not been quantified experimentally. Included among the present contributions to the organism's natural history in Barkley Sound are: 1) a quantified description of the organism's habitat at intervals throughout the year, as well as the physical characters of pools within each season; 2) an experimental examination of the apparent lethality of *C. trichotoma* on *T. californicus* individuals; 3) desiccation resistance as a mechanism by which *T. californicus* may persist in splashpools during temporary intervals of evaporation; and 4) the population density and approximate age structure of *T. californicus* populations throughout the year. Non-experimental discussion has also be presented on: 5) the potentiality of several dispersal agents endemic to the supralittoral habitat in Barkley Sound; and 6) the development of populations from small "founder" populations under temperature and salinity regimes representative of seasonal norms.

This general discussion will briefly summarize the findings of this thesis relative to previous studies of the ecology of *T. californicus* and its congeners, note omissions to the present work, and suggest avenues of further study.

SUPRALITTORAL HABITAT CONDITIONS IN BARKLEY SOUND

Observations of the supralittoral habitat occupied by *T. californicus* in Barkley Sound are not dissimilar to the general accounts for temperate splashpools provided elsewhere, particularly with regard to general shoreline features and the predominant taxa of macroalgae present (e.g., Fraser, 1936a; Kain, 1958; Gustavsson, 1972; Sze, 1981; Dethier, 1982; Morris and Taylor, 1983; Metaxas and Scheibling, 1993). Indeed, the most striking change in splashpool composition for the field sites is the seasonal

succession of macroalgae described in Chapter 1. However, this "visible difference" in splashpools may only be an ancillary consideration for a given splashpool's habitability when compared to: 1) the direct influence of wave action; and 2) the microflora present within each season.

Exposure to Wave Action: The paucity of *T. californicus* pools observed at tidal elevations less than *ca.* 3 m corresponds to the regular changes in the mean water level for the region. Between 3 and 5 m tidal elevation (from Chapter 1, the elevation at which 90% of *T. californicus* pools are found), metapopulations may either be decimated (washed-out) or randomly exchanged (mixed) by storm waves or the highest tides. As observed by Dybdahl (1994), such conditions may only exist for a few days per tidal cycle, and *T. californicus* become established only where isolated above the mean high tide level (see Figure 1.2). Above 5 m elevation, the opportunity for splashpools to be created and maintained is further lessened, and water deposits there are more likely replenished by precipitation and runoff. Similarly, Igarashi (1959) concluded that *T. japonicus* populations were younger and less stable in pools that were more frequently flushed by wave activity. Whether an increase in wave splash acts more significantly to decimate populations, or instead encourages the replenishment and genetic exchange between pools of a given metapopulation has not been sufficiently established for high-energy shorelines, but see Burton and Feldman (1981); Burton (1986); Brown (1991); Dybdahl (1994, 1995).

The irregular, incised features of the rocky shorelines of these study sites precludes the designation of generalized basin types (one suggested classification is illustrated in Figure C.1 and applied in Table C.1). Regardless of the designation for basin type (shape) used, any increase or decrease in the volume of pool water will change the basic bathymetry, and in turn, the calculation of pool water volume. Although an accurate determination of pool volume may be possible only by pumping all water out of the pool, this does not ensure sampling splashpool copepods any more efficiently than

with the methods of Chapter 5. Regardless of the sampling technique used, a reasonable estimate of pool volume is essential to derive *Tigriopus* population density within an ephemeral and highly variable pool volume to avoid erroneous conclusions of population flux based on individuals per volume sampled (Chapter 3). In contrast to oceanic samplers, for which an accurate determination of the water volume sampled is essential, the volume of water within which the sampler is deployed is the parameter of interest for estimating population density from littoral or supralittoral pools. Further, and distinct from most littoral pools, splashpools generally have a closed basin, which permits replenishment only from the surface. The infiltration of sea water through cracks or tunnels worn in the rock (possibly carrying predators or permitting an escape route for *T. californicus* from inhospitable conditions) is not evident, and so the nature of the air/pool interface becomes particularly important when considering the habitability of splashpools.

Certainly the volume, surface area, temperature and salinity of a pool will influence the habitability of the pool for *T. californicus* as well, but the extreme and recurrent flux in these parameters makes their selective influence difficult to track (but see Dybdahl, 1995). The large surface area-to-volume ratio of typical *T. californicus* pools in Barkley Sound (averaging 7.06, from Chapter 1) enhances the rate of evaporation but also provides a large interface with the atmosphere, providing an ample source of oxygen to support high densities of *T. californicus* and possibly counteract the activity of bacteria in isolated and stagnant pools. Additionally, the smaller volume and shallow depth of these splashpools serves to discourage or prevent habitation by larger predators such as sculpins and anemones (Dethier, 1980).

Vegetation and Food Resources: As with the physical parameters of pool water, *T. californicus* habitation is not apparently dependent upon any taxa of macroalgae. From Chapter 1, thriving populations of *T. californicus* are found in all seasons and regardless of the predominate vegetation (with the exception of *C. trichotoma*, from Chapter 2). Thriving populations were often found in pools containing no vegetation

beyond benthic diatoms and microalgae. Although the taxa and abundance of microflora can be expected to vary with season and tidal elevation (e.g., Sze, 1981; Metaxas and Lewis, 1992), an analysis of the microflora available to *T. californicus* in the splashpools of Barkley Sound was not part of the current thesis, hence an estimate of the natural food resources available to the organism is not included here (but see below). Gibor (1956), Provasoli et al. (1959) and the studies listed in Table 4.2 are among the legions of attempts to identify the 'preferred' food of *Tigriopus* species, but as with analyses of the tolerance of the congeners, treatments do not typically approximate natural conditions. Recent work by Carli et al. (1993) addresses *T. fulvus* feeding on *in situ* concentrations of *Vibrio* bacteria, and Lee and Taga (1988) present several strains of bacteria isolated from *T. japonicus* pools as "effective" food, but obviously the microflora available to the copepod will depend on season and location. The density of the ambient food resources will further depend on the stability of the pool and the amount of detritus or sediment it contains (see below).

Population Structure and Flux

The results of Chapters 4 and 5 agree favorably with previously published results for *T. californicus* field populations, including Egloff (1966) and Vittor (1971). From MacArthur and Wilson (1967, discussed in Vittor, 1971), the rapidity of organism development and extension of the reproductive interval will act to increase fecundity; in turn, fecundity is enhanced by increasing the number of clutches, rather than the number of clutches per female. Female *T. californicus* may produce up to 20 broods (Vittor, 1971), and with the species' remarkable fecundity and short generation time, could ostensibly produce 10 to 15 generations per year. While the clutch size *can* vary considerably between individuals or successive broods (see Comita and Comita, 1966, and the citations in Chapter 5), whether brood production *does* vary substantively will be a function of rearing temperature, food availability, and population density.

The results of this thesis suggest that this copepod reproduces throughout the year, but ostensibly attains a maximum *in situ* density of *ca.* 20 individuals · mL^{-1} in all seasons but winter. In winter, the number of colonized pools may be significantly reduced, but dense *T. californicus* populations may still result, even in very small pools containing no macroalgae. In addition, the extremely high proportion of gravid females present in such populations provides a remarkable potential for repopulation, should redistribution occur by hydrochore or biochore dispersal. Whether redistributed randomly by wave action (e.g., Dybdahl, 1994), trapped in a basin that ultimately evaporates, or carried as incidental ectoparasites on other organisms, *T. californicus* has demonstrated the ability to recover viable populations from a very small number of colonists (Vittor, 1971; Dybdahl, 1994; Chapter 3), and may procreate more successfully with intra-pool mates than via the random exchange of individuals between pools of a given metapopulation (Brown, 1991). Under hospitable conditions, the organism appears to flourish to an *in situ* maximum of *ca.* 20 · individuals mL^{-1}, whereupon egg deposition is inhibited and the cohort ages to become predominately adult males and females (possibly within 2 - 3 weeks, from Chapter 4).

It is at this point that other density-dependent processes may become more pronounced. To extrapolate the findings of cannibalism and maternal inhibition in high-density populations of *T. fulvus* (e.g., Lazarretto and Salvato, 1992; Kahan et al., 1988), *T. californicus* females apparently retain their egg sacs until the time of their eventual death. As mentioned in Chapter 3, dehydrated *T. californicus* do not drop their egg sacs, but hatching may occur soon after rehydration. This contrasts with the egg deposition and hatching that occurs almost immediately following sacrifice of gravid females, and may provide a more acute indication of death in the parent. Provasoli et al. (1959) also suggest that hatching in *T. californicus* and *T. japonicus* is induced by light, however I am not aware of experimental confirmation of this.

Burton and Feldman (1981) noted the difficulty in drawing conclusions about genetic structure from discrete observations. They suggest that since *T. californicus* is free swimming throughout its life history, dispersal might be expected, provided it is not too costly to the organism.[1]. Burton and Feldman (1981) further suggest that gene flow among all pools on an outcrop, with similarities in gene frequencies explained by founder effects or localized similarities in water properties and meteorological conditions.

Battaglia et al. (1978) also ascribed the genetic variability of *Tigriopus* under conditions of continued stress to individual plasticity. This work also provides a relatively rare genetic comparison between species of the genus - that of *T. fulvus* from Leghorn, Italy, with *T. brevicornis* from Tavvallich, Scotland, and a further comparison of *Tigriopus* with *Tisbe* species[2]. Battaglia et al. (1978) also noted that genetic variability decreases with temporal constancy of the environment; the more exacting the environment, the more strategies are based upon individual flexibility, not genetic plasticity. They conclude that *Tigriopus* likely has a fixation of generalist alleles, rather than any sort of genetic homeostasis. In exchange, the organism may have a low tolerance to biotic diversity, and be a poor competitor (Battaglia et al., 1978, and not, to my knowledge, confirmed experimentally). This is in agreement with theoretical natural selection in harsh or variable environments, whereby a few genotypes producing flexible or plastic phenotypes would be favored (*sensu* Pianka, 1970). Bottlenecks or decimation of populations are a common occurrence under the stressful conditions of the supralittoral zone, and genetic drift or founder effects have been suggested to explain the low genetic variability in field populations[3] (Egloff, 1966; Vittor, 1971; Battaglia et al., 1978; Burton and Feldman, 1981; Dybdahl, 1994).

Egloff (1966) found a mean egg development time of 2.4 days at 23°C, 4.8 days at 15°C and 8.2 days at 10°C for *T. californicus*, and calculates the total development

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[1] Brown (1991) determined that such outbreeding apparently is costly to *T. californicus*.
[2] Sampling of each species, however, occurred at only one field location.
[3] Bias inherent in the sub-sampling technique may also lead to bias in conclusions about sex or age.

time as 16.5 days at 23°C, or 27.5 days at 15°C. There is no periodicity of egg laying, and the potential for various life-history stages to be introduced to a pool at the same time may ensure that sex ratio variability and differential age structure are continued (Egloff, 1966). In general, reproductive rate increases with temperature and egg number, and decreases with sex ratio - with the influence of the former conditions being greater than that of the latter (Egloff, 1966). Egloff (1966) noted that while more females means enhanced growth of a population, predation by the females on nauplii will also increase. Hence, the absolute density of females in a population may be more significant than the female density relative to males (sex ratio). Certainly, newly-established populations of low density, as in recently colonized pools, would benefit from a decreased sex ratio (i.e., having more females). In populations growing more slowly, the percentage of males (which typically mature more quickly than females) would be expected to increase, while conversely, sex ratio decreases in rapidly growing populations, or those moving into increasingly stressful conditions (discussed in Egloff, 1966).

BEHAVIOR OF THE ORGANISM

Feeding: The feeding of *T. californicus* is not yet resolved. Although the organism has demonstrated feeding on a number of items in culture, the preferred diet for field populations has not been established. Although some studies have addressed the feeding preference of *Tigriopus* species (Gibor, 1956; Provasoli, 1959; Carli et al., 1993), I suggest that *T. californicus* is a detritivore, razing and subsisting upon the bacteria and benthic diatoms growing on the bottom of pools.

The feeding appendages of *T. californicus* appear to be ideally oriented to provide a "groove" for razing epiphytic growth from filamentous macroalgae such as *Enteromorpha* or *Scytosiphon* (L. Chatters, A. G. Lewis, pers. comm.). However, given the general paucity of macroflora in pools supporting thriving *T. californicus* populations (Chapter 1 and 2), it would appear that the copepod can feed equally well by browsing encrusting algae (such as *Ralfsia*-like crusts) or other phytobenthos attached directly to

the bedrock. Given this diverse potential for grazing, why *T. californicus* apparently does not browse *C. trichotoma* filaments is still unclear. As discussed in Chapter 2, either: 1) the filaments of *C. trichotoma* may not support the epiphytic growth preferred by *T. californicus*; or 2) given the rapidity with which *T. californicus* populations decline when exposed to *C. trichotoma*, some chemical agent that is deleterious to *T. californicus* may indeed be responsible.

Swimming: A dive-and-cling swimming response to shadows or pressure disturbances has been observed in *Tigriopus californicus* (Egloff, 1966; Vittor, 1971) and for harpacticoid copepods in general (Hicks and Coull, 1983). While the organism has been observed to 'crawl' easily over a variety of surfaces and textures, it is doubtful that the behavior is sufficient to retain the organism's position in a pool, especially during storm events. Wash-out of pools is noted by Igarashi (1959), Dethier (1980), Burton and Feldman (1981), but as stated above, it is not known how long *T. californicus* might remain in the plankton without being culled by any number of agents.

The magnitude and rapidity of the 'dive and cling' response of *T. californicus* to pool disturbance has not been tested for harpacticoids (but see Richardson, 1992). As a natural reaction to escape predation or survive wave disturbance, the dive and cling behavior also serves to confound the accurate census of splashpool populations. While the pipette method described in Chapter 5 still under-represents actual abundance to some degree, it does draw material from along the substratum, making it more effective than scoops or dipnets for sampling all life-history stages. A waterproof video camera could be used in a splashpool to observe the use of the water column by the various life-history stages under undisturbed conditions, provided a suitable lens and camera housing could be found for use on high-energy shorelines.

Thigmotaxis: As noted above, the clinging behavior noted in response to pool disturbance may also assist in the biochore dispersal of *T. californicus*. By clinging to the carapaces of crabs, the gills of fish, or even the feet and plumage of shore birds, it is

possible that a few individuals could be dispersed far beyond the inshore circulation of wave activity. *Tigriopus californicus* nauplii are observed to be thigmotactic when offered to larval fishes; *T. californicus* respond aggressively to the presence of fish, often grasping the gills and operculae, although the copepodite stages have been successfully used in the diet of older fish larvae (Morris, 1956; reviewed by May, 1970). When not consumed by fish, it is possible that this same behavior may assist in distributing the copepods in limited numbers on migrating fish. However again, unless eventually released very close to a suitable refuge, it is doubtful that the copepod could survive long in the water column.

Chemotaxis: Particularly in aquatic environments, chemically-mediated behavior may promote either the dispersal or homing response of an organism. Although sexual dimorphism is not visually apparent in *T. californicus* until the C-IV stage, males appear able to recognize 'potential females' as early as the C-I or C-II stage; chemical signaling by the female may be the stimulus for these responses; male specimens do not appear to release any signaling compounds (Lazzaretto et al., 1990). Lazzaretto et al. (1990) tested *T. fulvus* for 1) offspring recognition and 2) species recognition (between *T. fulvus*, *T. californicus* and *T. brevicornis*) and found the response to previously inhabited containers was species specific, and that aggression of the females was noted towards non-related nauplii (a behavior also noted by Egloff, 1966). Further, nauplii placed in medium without gravid females were noted to 'disappear,' while late N-stage and copepodite stages did not (Lazzaretto et al., 1990).

The work of Kahan et al. (1988) propose the transmission of inhibitory messages to the egg sac in *T. japonicus*. This work further suggested that the 'hook-like' structures leading into the egg sac, and described by Fahrenbach (1962) may be the structure conducting such messages from the mother. At high population densities (greater than 50 individuals $\cdot L^{-1}$), the deposition of eggs appears to be inhibited, while the number of nauplii hatching was observed to increase over time. The laying of eggs then appears to

be inhibited, not promoted. In field populations, an inordinate number of egg-carrying females is noted, supporting this notion. However, regardless of density, eggs will hatch to nauplii within an hour once the mother is killed.

Once relocated into a new pool, chemical secretions may provide an indication of the pool's habitability. Bozic (1975) describes an 'aggregation pheromone,' whereby *Tigriopus* (I assume *fulvus*) demonstrates a preference for vessels containing water previously inhabited by the same species. Dethier (1980) proposes that displaced *T. californicus* may be able to locate their home pool or detect refugia which previously sustained copepod populations. I have observed *T. californicus* to congregate around previously-inhabited Petri dishes mounted in 25 L aquaria flooded with artificial sea water (unpublished data) and do not dismiss chemically-mediated behavior as an effective agent over short distances and under tranquil conditions. From Bozic (1975) chemical secretions by as few as 20 copepods have permeated smooth, solid test chambers in as little as 15 hours; Dethier (1980) suggests the concentration of chemical signals from a densely populated pool could be considerable. As discussed in Chapter 2, the combination of chemical agents in a stagnant splashpool must be diverse and confusing to a potential colonist. For individuals washed out of a pool on an isolated outcrop, it is even more unlikely that attractive scents could be detected by the copepod and followed successfully back to a previously inhabited pool, given the size of the individual against that of the maelstrom.

Distribution of the Genus Among Similar Habitats

Observations of the ecosystem particular to Barkley Sound have provided several potential agents for dispersing *T. californicus,* some suggested here for the first time. The innate physical tolerance, comparatively short generation time, and high fecundity of *T. californicus* would allow it to readily colonize any habitable coastal pools, with localized extinction and vicariance events eventually producing the current global distribution for *Tigriopus* species. From Chapter 3, only 100 to 150 *T. californicus*

retained by a bird (or birds) foraging in the supralittoral zone would be sufficient to provide dispersal in this manner. At the *in situ* population densities *T. californicus* may attain (often in excess of 20 individuals · L^{-1}, with a mean in excess of 750 individuals · L^{-1} over much of the year), such estimates are not unreasonable and provide an avenue worth further examination.

Figure GD.1 provides a simplified account of how *T. californicus* and its congeners may have become dispersed by avian carriers within the past *ca.* 8,000 years (i.e., utilizing the current coastlines and position of continental land masses in the Northern Hemisphere). For the current discussion, Figure GD.1 does not presume to illustrate the origin or cladistics of *Tigriopus* congeners, but illustrates how the copepod could be transported incidentally along the migratory corridors of several bird species.

For all practicable purposes, metapopulations of *T. californicus* may still be considered "genetically isolated [and] currently undergoing independent evolution," as Burton (1986, p. 532) suggested. From the limited data available for the current thesis, the potentiality of avian carriers is put forth as reasonable speculation; gradual dispersal or punctuated instances of gene flow by avian carriers would be virtually impossible to detect without radio-tracking and recapture of the birds, and genetic or vital stain comparisons of the copepods themselves.

Follow-up experimentation on the viability of these various agents is clearly needed, with particular attention to 1) the transport of *T. californicus* by incidental vertebrates and invertebrates; and 2) the potential for metapopulation dispersal by longshore transport. Suggestions include detailing the home range of crabs, birds, or shoreline vertebrates that traverse rocky shores occupied by *T. californicus* metapopulations. The resistance to desiccation noted in Chapter 3 provides a plausible mechanism for the organism to survive inhospitable conditions, and perhaps even extended air transport. Once deposited in a new pool, the re-animated individuals possess an equally remarkable potential to rapidly increase their numbers (Chapters 4 and 5), and

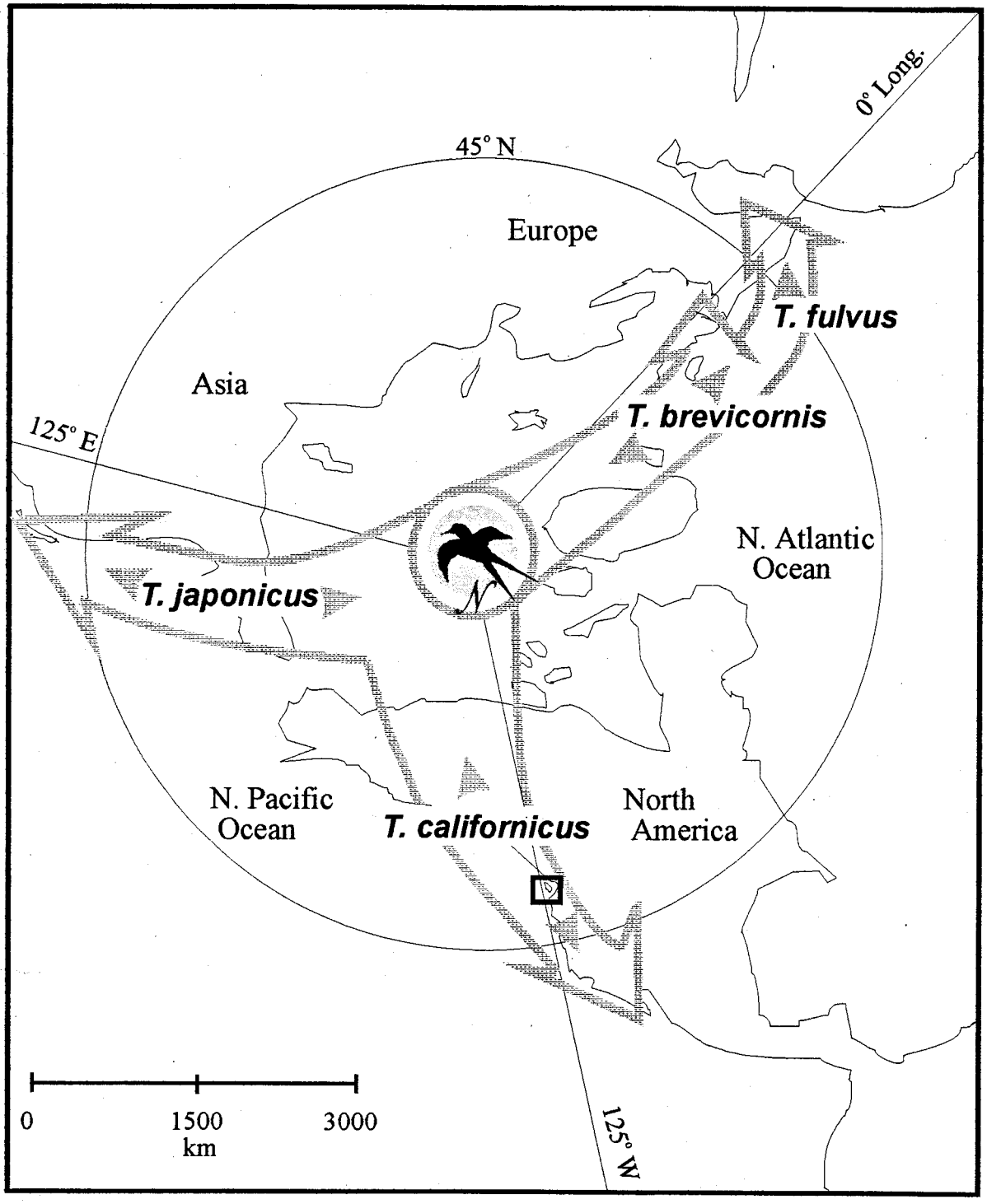

FIGURE GD.1. Proposed dispersal routes of *Tigriopus* congeners by avian carriers. All currently extant species may well have arisen from a single locale, then dispersed and becoming genetically isolated under the influence of local selection pressures. Square indicates the location of the current study area.

providing a theoretically stable colonizing population with a diversity of life-history stages.

TOLERANCE OF THE ORGANISM

Apropos to the extreme conditions of its natural habitat, *Tigriopus* expresses considerable euryhaline and eurythermal endurance. Temperature and salinity act as selective agents on polymorphism as well as genetic variability (Battaglia, 1970). In both field and laboratory studies, water temperature can influence differences in the equilibrium frequencies of genes which control polymorphism (Battaglia and Lazzaretto, 1967, as cited in Battaglia, 1970).

Given this, a fundamental impetus for the series of observations and experiments presented in this thesis is to assist the development of future laboratory studies that provide experimental regimes representing more closely the natural conditions found in the habitat of *T. californicus*. Numerous studies using *T. californicus* have provided data on the organism's tolerance and response to a broad range of temperature and salinity regimes, but these have not necessarily been indicative of *in situ* conditions:

Salinity: McDonough and Stiffler (1981) tested the organism's osmoregulation over a salinity range of 60 to 300‰. Huizinga (1971) found a salinity tolerance in *T. californicus* over a range of 21.2 to 75.3‰, with 'optimum' activity at 42.3 to 47‰. In contrast, Takano (1968) found optimal salinity conditions for *T. japonicus* to be slightly less than 100% sea water. Ranade (1957) tested the tolerance of *T. fulvus* over a salinity range of 0 to 225‰ at 16-18 °C. Survival of individuals was reported as 60 hours at 98‰, 30 hours at 180‰ and 3 hours at 255‰, although salinities in excess of 90‰ produced 'apparent death' in most individuals. Issel (1914) found *T. fulvus* to have a tolerance to salinities in excess of 190‰ and also notes a condition of 'apparent death,' from which the organism can awaken and regain normal activity when the water is sufficiently diluted. Egloff (1966) found *T. californicus* to resume normal activity

following dilution from 334‰, and Kasahara and Akiyama (1976) reported similar observations for *T. japonicus*, however Chapter 3 of this thesis has provided the first quantified account of this response (to duration and life-history stage) and the first record of *in situ* re-animation for the genus.

Ranade (1957) also noted that dried splashpools replenished only by rain water could retain populations of *T. fulvus*, an observation which is further discussed in Chapter 3. Indeed, the response of the organism to fresh water has been less clearly documented, and may be even more deterministic to the organism's survival than hypersaline conditions. Ranade (1957) noted *T. fulvus* to perish in distilled water within 84 h. Igarashi (1960) tested *T. japonicus* over a range of 5 to 180% sea water, and found a lower salinity tolerance of 3.4‰; Lee and Hu (1981) provided an even lower threshold of 1.8‰ for the same species, and I have found *T. californicus* populations in pools with a salinity of <1‰, as determined by refractometer or measurements of conductivity. Igarashi (1960) found gravid *T. japonicus* to lose their eggs sacs at low salinities, as well as a delay in spawning recruitment (relative to 80% and 100% sea water) but found no apparent correlation between salinity and sex ratio.

Igarashi (1960) also found that spawning recruitment occurred earlier at 80% and 100 % sea water, which compares with Takano's (1968) results. Conversely, Egloff (1966) found a negative correlation between salinity and sex ratio, indicating that *T. californicus* females are more tolerant to high salinities. In field populations, higher pool salinity (from evaporation) corresponds to evaporation, which is enhanced at higher temperatures. Egloff (1966) and Vittor (1971) find more males are produced at higher temperatures (with a shorter generation time, egg to C-VI adult), hence the overall effect on sex ratio may be inconsequential, as the time of relatively higher salinity tolerance for females corresponds to the comparatively greater production of males. As the reproductive potential of the population is thus enhanced, individuals are also constrained

to a smaller volume of water as the pool evaporates, producing the sometimes phenomenal population densities reported in the literature and in the present thesis.

The salinity of a splashpool may be quickly reduced by intense precipitation or even normal sea water waves diluting a hypersaline water deposit, while increases in salinity may occur from 1) sea water infiltrating a pool filled with comparatively fresh water; 2) runoff carrying salt encrustation into a pool; or 3) gradually, from evaporation. Egloff (1966) performed natural (evaporative) salinity changes, beginning at 43‰. Activity was still evident at 102‰ (37 days later), but ceased at 200 ‰ (44 days). The experiment was ceased at 56 days at 334‰, and the organism was re-animated by normal sea water. Egloff (1966) also experimented with *T. californicus* survival after 30 minutes of exposure to desiccation at 60 and 100% relative humidity, and found egg sacs to respond best to drying, while nauplii experienced the highest mortality. I did not find eggs to respond following drying, and noted copepodites to revive the most quickly from re-hydration, most likely from their larger surface area: volume ratio (see Chapter 3).

Temperature: The small volume and high surface area of a typical splashpool makes it particularly susceptible to changes in temperature due to solar heating, cooling by wind, or even complete freezing. Ranade (1957) reports *T. fulvus* heat tolerance at over 40°C. He also observed a 'death point' temperature at which *ca.* 75% of the experimental individuals died within a temperature change of 0.1°C. He does not elaborate further on this observation, and used only two samples. Kontogiannis (1973) described acquisition of heat tolerance in *T. californicus* from 0 to more than 30°C, including thermal shocks of 10°C. A lower temperature threshold has not been published, however in casual experimentation, I have suspended *T. californicus* in ice, to have it resume normal activity once thawed. For the current field sites, it is doubtful that pool temperatures ever exceed 30 to 35°C, however this does not lessen the influence of evaporation from exposure. Moreover, temperature changes occur much more quickly,

and one would expect thermal shock to be more common and more extreme than haline shock.

Excepting the action of pollutants, a rapid change (cooling) in pool temperature from wave splash may be the only explanation for observations of splashpool *Tigriopus* populations which appear to be all, or apparently all, dead. As with any microscale changes in pool water condition, the small, isolated volume of splashpools leaves them particularly susceptible to the action of pollutants. O'Brien et al. (1988) found *T. californicus* able to tolerate cupric ion activity two to three orders of magnitude greater than other copepods, including *Acartia, Calanus, Euchaeta, Labiodocera* and *Metridia* spp.[4] Again, while providing impressive results of what the organism *can* tolerate, few of these experiments have been devised with the intent of approximating the conditions found in supralittoral splashpools (i.e., what the organism *does* tolerate).

Somewhat paradoxically, given the demonstrated hardiness of the genus to pollutants and physico-chemical stress, *Tigriopus* congeners continue to be utilized as indicator species for pollutant studies, including population response to contaminated sediments (LeDean and Devineau, 1985; Pacquet and Lacaze, 1988; Misitano and Schiewe, 1990; Pacquet and Lacaze, 1990; Pavillon et al., 1990), even though sediment accumulation is rarely observed in supralittoral pools, at least in the study sites I selected in Barkley Sound. As noted by O'Brien et al. (1988), the use of an exceptionally tolerant organism as an indicator species in bioassays or lethality tests can, depending on the study, significantly bias the recommendations derived from the observed results. While still formidably suited to studies in ecology, fisheries, genetics, and use as a bioassay organism, further empirical analyses of the organism's response to realistic and controlled *in situ* environmental conditions are clearly needed if the ecology of this copepod is to be detailed further.

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[4] Perhaps not surprisingly, since copper and chlorine levels are typically much higher in splashpools, due to frequent and repeated evaporation of a comparatively small volume.

To conclude, I must extend my regards to Dr. Brian Marcotte, whom I have never met, for his 1977 dissertation "The ecology of meiobenthic harpacticoids (Crustacea, Copepoda) in West Lawrencetown, Nova Scotia" (Dalhousie University, Halifax, N.S.). Though addressing considerably different aspects of harpacticoid ecology, and distanced from the present thesis by nearly two decades and the entire breadth of this country, Marcotte's work was instrumental in the prose and process of the current manuscript. It is Marcotte's work that first acquainted and attracted me to the field of harpacticoid biology, and it remains nearly without equal as a tome that so completely discusses its subject while paying homage to the scientific, artistic, and humanistic factors inspiring endeavors such as ours. This philosophy is embodied in the following excerpt from Marcotte's (1977) preamble:

> The world of these ancient argonauts is a thousand micron sea.
> It is a world of flake and stone, or crystalline herbs and truffled gardens, of thimble mountains and ever-shifting sand.
> It is not the pickled muds museum's house,
> just as human society is not a city morgue.
>
> Rather, their world can only be understood as they would live in it: sense it, explore it, eat, rest, reproduce.
> Meiobenthic harpacticoids are not distributed in space and time, they *are* space and time. Their physiology, morphology and behavior define the dimensional space in which they live and of which their evolutionary history can only hint.
>
> Meiofauna adapt not in time but embody it; size and community structure are the sensible beat of their clock. In short, their physics exists only in so far as they live, and our understanding of them exists only in so far as we can take on their life.
> For this end, the present thesis begins.
>
> — B. M. MARCOTTE (1977)

Appropriately, with these same words, the present thesis ends.

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APPENDIX A: LOCATION MAPS

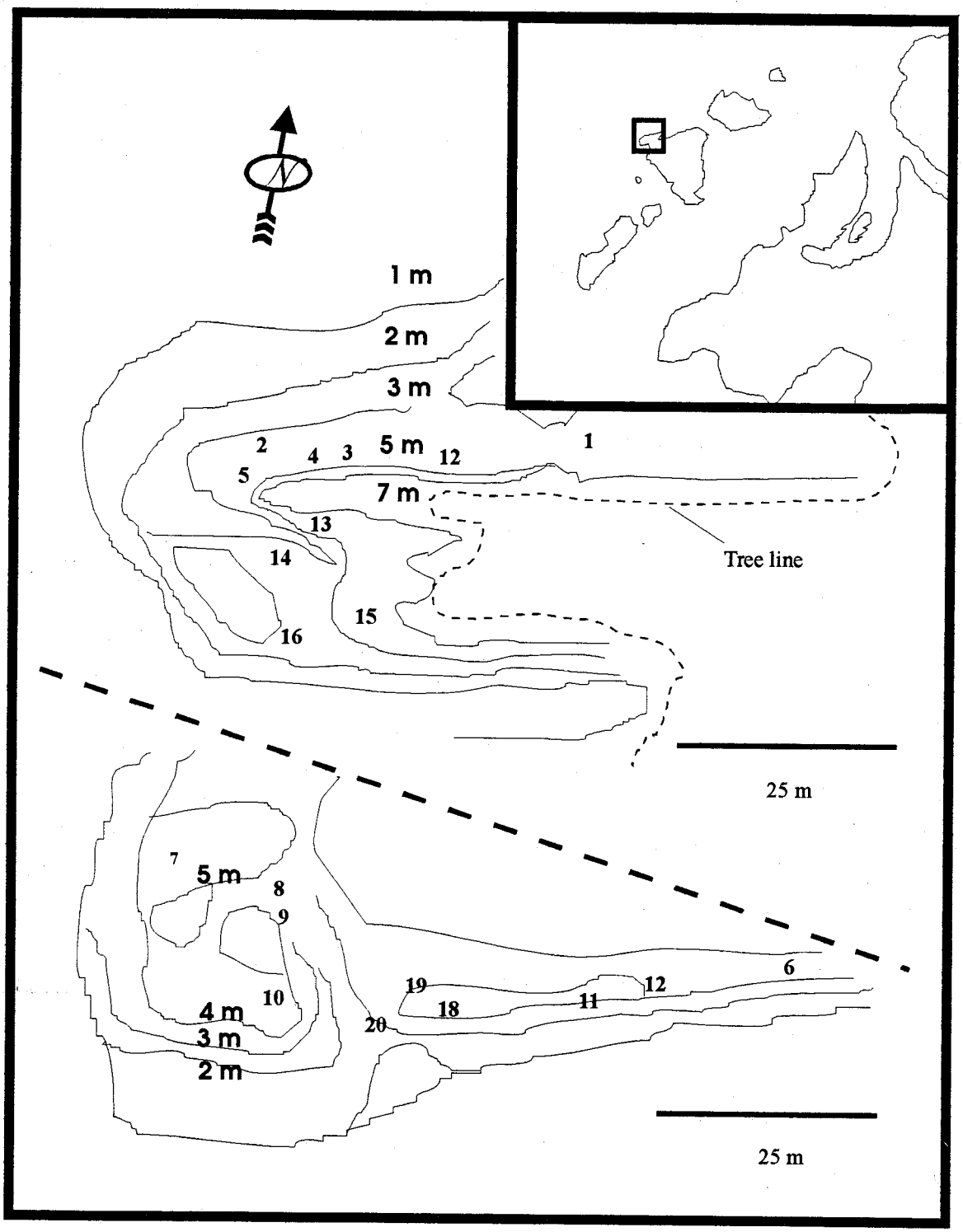

FIGURE A.1. Location of study pools on Diana Island. Numbers correspond to the designation and position of pools monitored over the duration of the study. Upper portion illustrates to the northeast portion of Kirby Point; lower section illustrates the southwest portion of Kirby Point on the western edge of the island. Thumbnail map shows relation of study site to the area described by Figure 1.1.

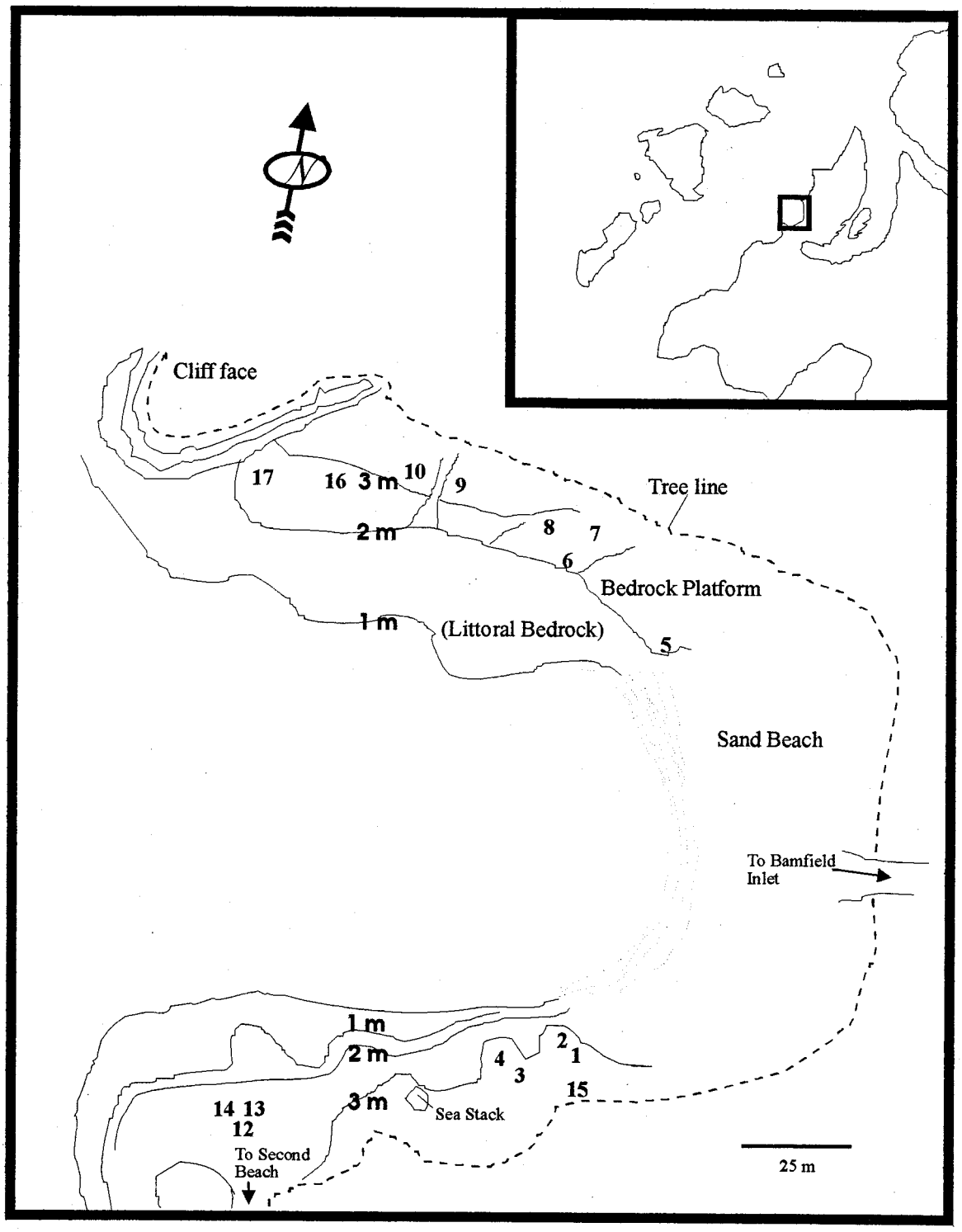

FIGURE A.2. Location of study pools on First Beach. Numbers correspond to the designation and position of pools monitored over the duration of the study. Thumbnail map shows relation of study site to the area described by Figure 1.1.

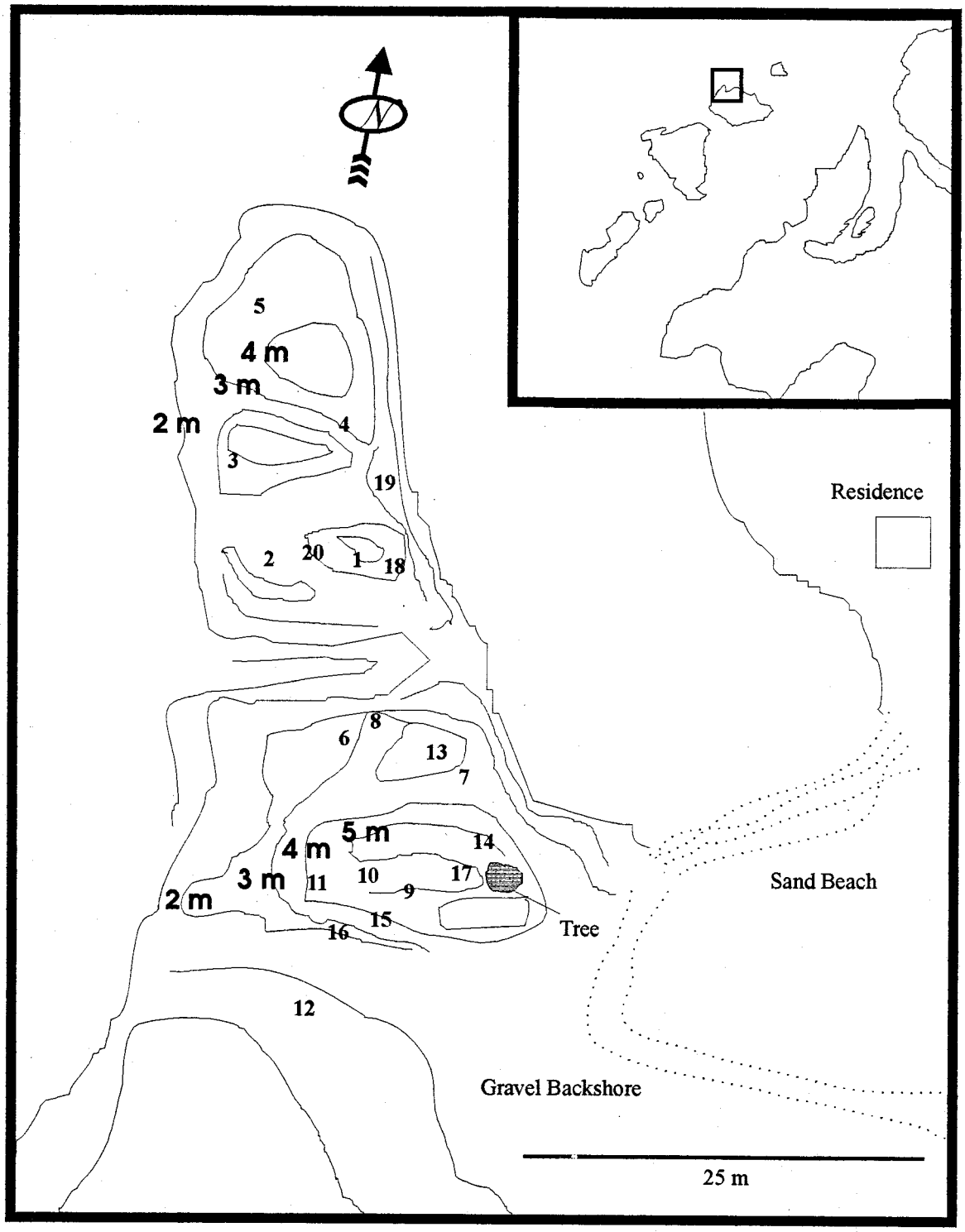

FIGURE A.3. Location of study pools on Helby Island. Numbers correspond to the designation and position of pools monitored over the duration of the study. Thumbnail map shows relation of study site to the area described by Figure 1.1.

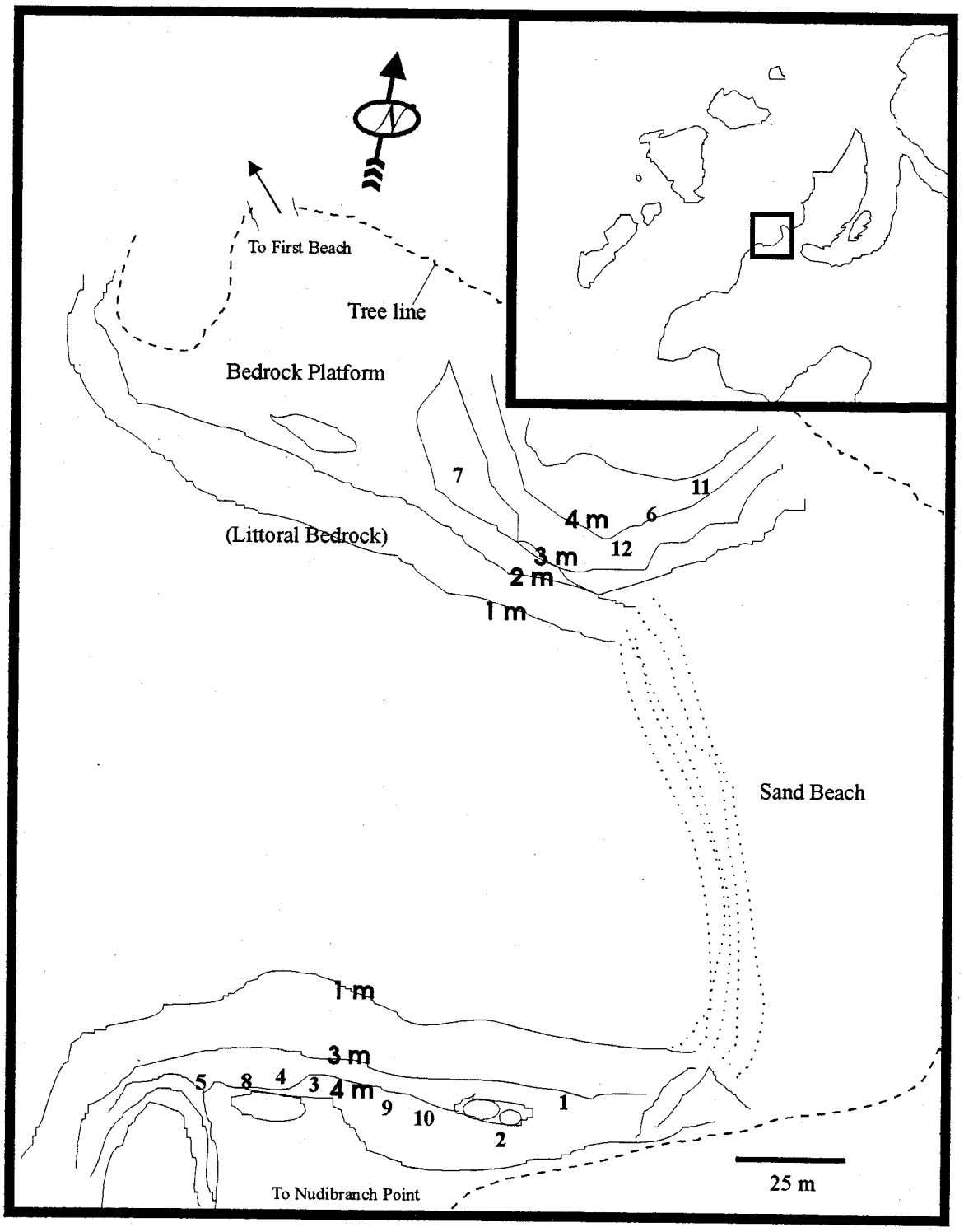

FIGURE A.4. Location of study pools on Second Beach. Numbers correspond to the designation and position of pools monitored over the duration of the study. Thumbnail map shows relation of study site to the area described by Figure 1.1.

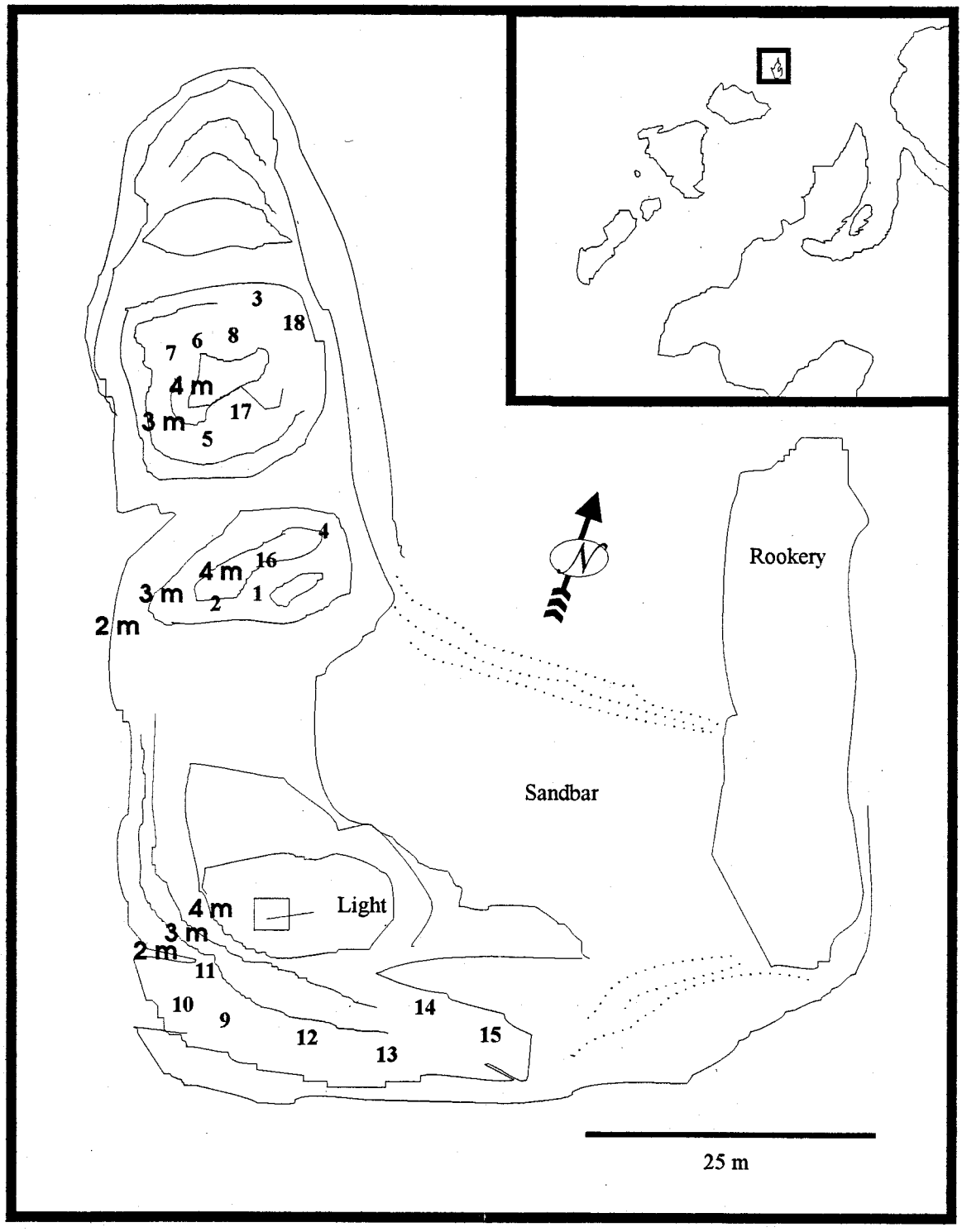

FIGURE A.5. Location of study pools on Wizard Islet. Numbers correspond to the designation and position of pools monitored over the duration of the study. Thumbnail map shows relation of study site to the area described by Figure 1.1.

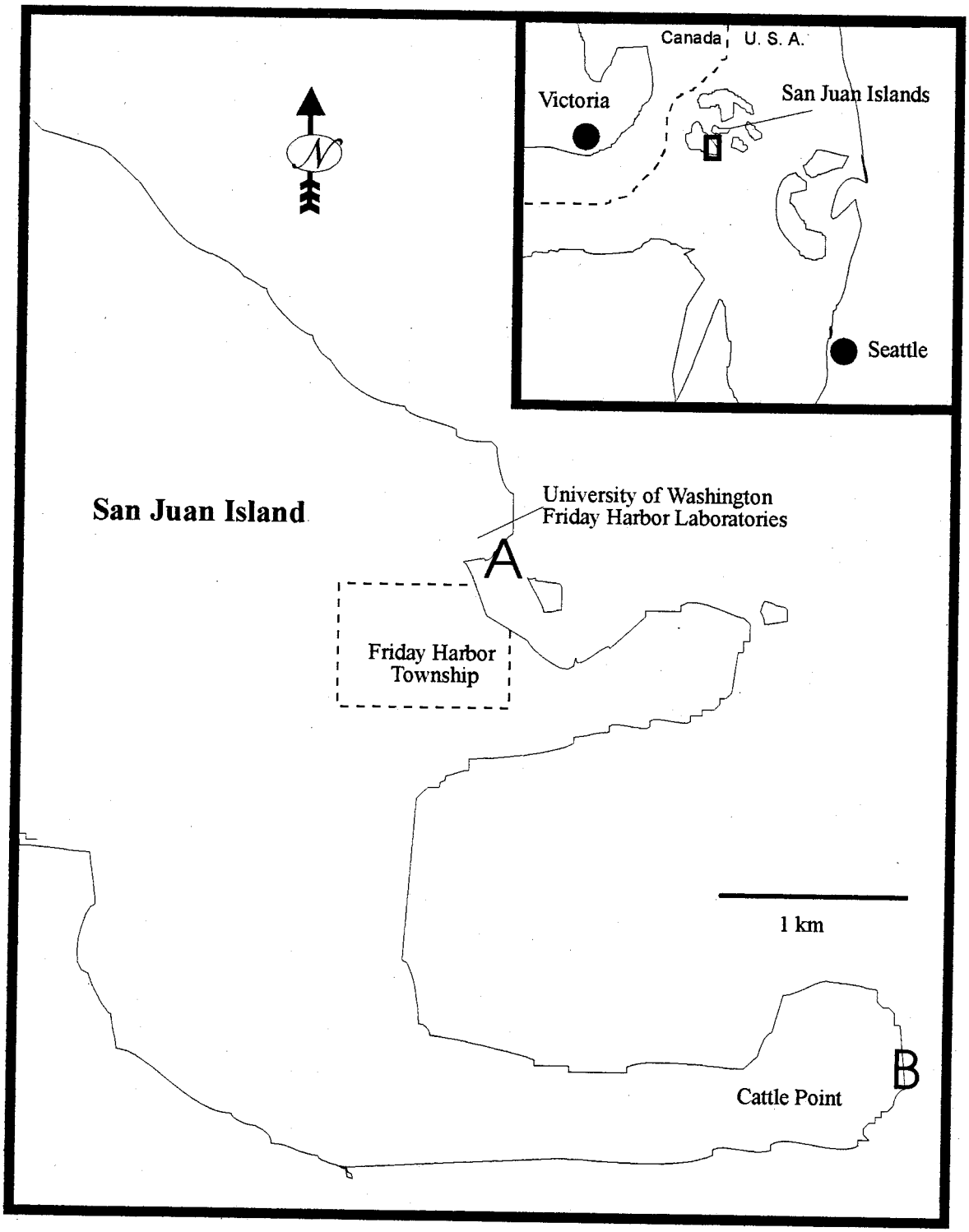

FIGURE A.6. Location of supplemental study pools on San Juan Island, Washington. A and B correspond to the location of $n = 6$ pools at each site, monitored hourly for changes in temperature, salinity, and *Tigriopus* abundance during February, 1995. Pools at each site were located within *ca.* 10 m of each other. The Friday Harbor Laboratories location represented a sheltered coastline, in contrast to the comparatively exposed coastline at Cattle Point. Thumbnail map illustrates the position of the San Juan Islands group (not illustrated in Figure 1.1).

APPENDIX B: WEATHER AND TIDE DATA

TABLE B.1. Rainfall at Bamfield (in mm) 1973-1986*. Source: Western Canada Universities' Marine Biological Station (WCUMBS), Bamfield, B.C.

YEAR	JAN.	FEB.	MAR.	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1973	507.7	199.6	304.0	59.7	216.4	124.2	46.5	17.0	89.4	384.6	428.2	605.3
1974	429.3	576.3	590.8	226.6	273.6	98.8	130.8	3.8	82.6	82.9	465.1	530.4
1975	296.7	218.7	250.2	138.9	168.2	88.9	16.0	203.2	7.9	674.4	661.7	474.0
1976	400.3	406.4	383.0	147.8	180.3	112.3	67.3	140.5	55.4	234.1	157.2	315.5
1977	185.2	367.8	330.7	130.3	220.7	59.4	60.2	67.8	84.3	322.8	502.9	268.0
1978	236.5	214.9	283.7	153.4	124.0	107.7	5.3	254.0	213.9	100.3	218.4	226.8
1979	89.9	518.2	216.7	140.5	100.8	83.3	88.9	30.5	230.4	242.3	223.3	639.3
1980	217.9	312.4	248.9	227.6	58.1	62.4	119.6	65.8	165.1	134.0	491.6	603.0
1981	128.0	319.6	238.1	388.0	136.0	195.6	284.0	56.0	222.5	425.4	389.8	382.0
1982	510.8	521.4	171.4	216.9	42.8	52.0	59.0	43.2	79.8	426.2	340.2	446.2
1983	547.4	620.6	425.4	111.8	104.0	128.2	213.6	43.2	88.8	221.6	662.6	167.4
1984	513.6	413.4	290.6	327.2	265.0	83.2	19.0	55.8	144.2	447.6	435.0	309.8
1985	76.6	175.6	247.1	202.2	66.2	49.7	8.2.	45.2	91.4	409.2	130.6	155.6
1986	450.6	358.0	435.2	219.0	323.2	107.4	52.0	12.0	88.8	123.6	460.2	489.6

* Data for these particular years are presented as they were readily available and are often referenced from WCUMBS Bamfield.

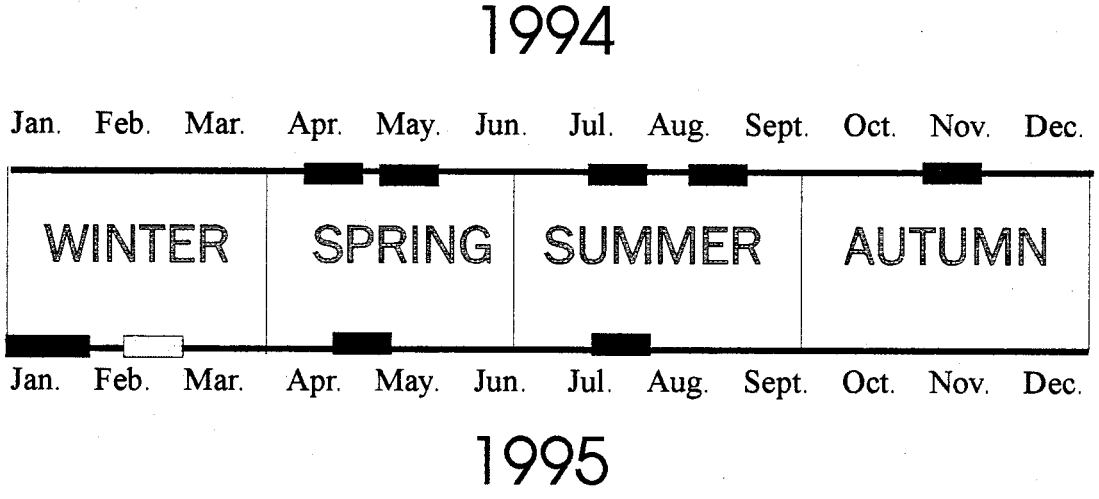

FIGURE B.1. Seasonal sampling intervals in 1994 and 1995. Blackened sections represent sampling periods in Barkley Sound, typically of six to 18 days duration. Half-tone section indicates timing of supplemental data collection on San Juan Island in Washington State.

TABLE B.2. Summary of key weather conditions during sampling intervals. All values presented as mean values ± 1 standard error from daily weather data, as available. Detailed weather data could not be obtained for all sampling intervals, including those at Friday Harbor Marine Laboratories (Friday Harbor, WA), in February, 1995. Source: Environment Canada weather offices in Port Alberni and Vancouver, B.C.

PARAMETER	JULY, 1994	AUGUST, 1994	NOVEMBER, 1994	JANUARY, 1995
Daily High (°C)	18.0 ± 0.7	19.5 ± 0.9	10.4 ± 0.5	9.3 ± 1.7
Daily Low (°C)	9.8 ± 1.6	9.1 ± 1.3	2.5 ± 2.0	1.7 ± 4.6
Mean (°C)	13.9 ± 4.4	14.3 ± 5.6	6.4 ± 4.4	5.5 ± 5.2
POP (Probability of Precipitation)	15 ± 5 %	25 ± 20 %	65 ± 40 %	65 ± 40 %
Actual Precipitation (mm/day)	0	0.6 ± 0.8	10.7 ± 17.4	8.8 ± 9.1
Wind	Moderate Northwesterlies (15 knots)	Light and Varible (5 - 10 knots) Moderate Northwesterlies	Shifting winds, Northwesterlies to 20 knots	Moderate to Strong Southeaterlies (15 - 25 knots)
Sunrise	05:30	06:28	07:11	08:16
Sunset	21:26	20:23	17:02	16:43
Hours of Sun	7.6 ± 3.0	8.9 ± 2.4	3.6 ± 4.2	2.5 ± 3.0
Ultraviolet Index	6.9 ± 0.2	5.6 ± 0.5	N/A	N/A

TABLE B.3. Tide conditions in Barkley Sound during sampling. Values (in meters) corrected for local conditions by DFO (1994, 1995) and N. J. Wilimovsky. HHW = Highest, High Water; LHW = Lower, High Water; HLW = Higher, Low Water LLW = Lowest, Low Water. Time of highest and lowest daily tide also noted as on table (correct +1 hour for daylight time: 3/4/94 to 30/10/94; 2/4/95 to 29/10/95).

Month	Date	HHW		LHW	HLW	LLW	
April	1	3.5	03:25	2.7	1.5	0.5	10:22
1994	2	3.2	04:29	2.6	1.6	0.7	11:28
	3	3.0	05:38	2.6	0.8	0.8	12:40
	4	2.9	06:57	2.7	1.6	0.9	13:52
	5	2.9	08:14	2.8	1.6	0.9	14:54
	6	2.9	22:08	2.9	1.4	0.9	15:44
	7	3.0	22:43	3.0	1.2	0.9	16:26
	8	3.1	23:14	3.0	1.0	1.0	04:51
	9	3.2	23:42	3.0	1.0	0.9	05:29
	10	3.0	12:17	3.0	1.1	0.8	06:03
	11	3.3	10:00	3.0	1.2	0.7	06:37
	12	3.3	00:38	2.9	1.3	0.7	07:10
	13	3.3	01:07	2.8	1.4	0.7	07:43
	14	3.3	01:37	2.7	1.5	0.7	08:18
	15	3.2	02:10	2.7	1.6	0.8	08:55
	16	3.1	02:47	2.6	1.7	0.9	09:37
	17	3.0	03:30	2.5	1.8	0.9	10:26
	18	2.9	04:24	2.5	1.7	1.0	11:23
	19	2.8	05:33	2.6	1.0	1.0	12:27
	20	2.8	20:12	2.7	1.6	1.0	13:31
	21	3.0	21:01	2.8	1.4	0.9	14:29
	22	3.2	21:45	2.9	1.1	0.9	15:22
	23	3.5	22:28	3.0	0.9	0.8	16:11
	24	3.7	23:10	3.1	0.9	0.4	04:58
	25	3.8	23:53	3.1	0.9	0.2	05:46
	26	3.1	12:56	3.1	1.0	0.0	06:33
	27	3.8	00:38	3.1	1.1	-0.1	07:21
	28	3.8	01:24	3.0	1.2	0.0	08:09
	29	3.6	02:12	2.9	1.3	0.2	09:00
	30	3.4	03:05	2.8	1.5	0.4	09:54
	Highest	3.8		3.1	1.8	1.0	
	Lowest	2.8		2.5	0.8	-0.1	
	Avg.	3.2		2.8	1.3	0.7	
	s.d.	0.3		0.2	0.3	0.3	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
May	1	3.1	04:03	2.7	1.6	0.6	10:59
1994	2	2.9	05:14	2.7	0.8	0.8	12:02
	3	2.8	19:47	2.7	1.5	0.9	13:05
	4	2.9	20:39	2.7	1.4	1.1	14:04
	5	3.0	21:21	2.6	1.2	1.1	02:54
	6	3.0	21:58	2.7	1.2	1.1	03:44
	7	3.1	22:31	2.7	1.2	0.9	04:27
	8	3.2	23:02	2.8	1.3	0.8	05:06
	9	3.3	23:33	2.8	1.4	0.6	05:41
	10	2.8	12:40	2.8	1.4	0.6	06:16
	11	3.3	00:04	2.8	1.5	0.5	06:50
	12	3.3	00:36	2.8	1.5	0.5	07:23
	13	3.3	01:10	2.7	1.6	0.5	07:58
	14	3.2	01:46	2.7	1.6	0.6	08:34
	15	3.1	02:25	2.7	1.6	0.6	09:13
	16	3.0	03:10	2.7	1.6	0.7	09:56
	17	2.9	04:04	2.8	1.6	0.8	10:46
	18	2.8	18:28	2.7	0.9	0.9	05:09
	19	3.0	19:24	2.6	1.4	1.0	12:41
	20	3.2	20:17	2.6	1.2	1.0	13:42
	21	3.4	21:07	2.7	1.1	0.9	02:52
	22	3.5	21:55	2.7	1.1	0.5	03:49
	23	3.7	22:42	2.9	1.1	0.2	04:41
	24	3.8	23:29	3.0	1.1	0.0	05:30
	25	3.0	12:47	3.0	1.2	-0.1	06:18
	26	3.8	13:37	3.0	1.2	-0.1	07:06
	27	3.7	01:05	3.0	1.2	0.0	07:53
	28	3.5	01:56	3.0	1.3	0.1	08:41
	29	3.3	02:48	2.9	1.4	0.3	09:30
	30	3.1	03:44	2.9	1.4	0.6	10:20
	31	2.9	17:54	2.8	0.8	0.8	11:12
	Highest	3.8		3.0	1.6	1.1	
	Lowest	2.8		2.6	0.8	-0.1	
	Avg.	3.2		2.8	1.3	0.6	
	s.d.	0.3		0.1	0.2	0.4	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
July	1	2.9	18:42	2.4	1.3	1.3	12:03
1994	2	2.9	19:32	2.3	1.5	1.2	01:32
	3	3.0	20:22	2.3	1.6	1.1	02:33
	4	3.0	21:10	2.3	1.6	0.9	03:28
	5	3.1	21:54	2.4	1.6	0.8	04:16
	6	3.2	22:35	2.6	1.6	0.6	04:57
	7	3.3	23:15	2.7	1.5	0.5	05:34
	8	3.4	23:54	2.7	1.5	0.4	06:09
	9	2.8	13:10	2.8	1.4	0.4	06:42
	10	3.4	00:34	2.9	1.3	0.4	07:15
	11	3.3	01:15	3.0	1.2	0.4	07:50
	12	3.2	01:59	3.1	1.2	0.5	08:26
	13	3.1	15:38	3.1	1.1	0.6	09:05
	14	3.2	16:24	2.9	1.0	0.7	09:48
	15	3.2	17:14	2.7	0.9	0.9	10:36
	16	3.2	18:11	2.5	1.1	1.1	11:32
	17	3.3	19:12	2.4	1.3	0.8	01:05
	18	3.3	20:15	2.4	1.4	0.6	02:16
	19	3.4	21:15	2.5	1.4	0.4	03:20
	20	3.5	22:11	2.7	1.3	0.3	04:17
	21	3.5	23:04	2.8	1.2	0.2	05:07
	22	3.5	23:54	2.9	1.2	0.1	05:52
	23	3.0	13:01	3.0	1.1	0.1	06:35
	24	3.5	00:41	3.1	1.1	0.2	07:15
	25	3.4	01:27	3.1	1.1	0.4	07:53
	26	3.2	02:11	3.1	1.1	0.6	08:30
	27	3.0	15:30	3.0	1.2	0.8	09:05
	28	3.0	16:07	2.7	1.2	1.0	09:40
	29	2.9	16:47	2.5	1.2	1.2	10:17
	30	2.9	17:33	2.3	1.4	1.4	11:00
	31	2.8	18:28	2.2	1.6	1.2	00:36
	Highest	3.5		3.1	1.6	1.4	
	Lowest	2.8		2.2	0.9	0.1	
	Avg.	3.2		2.7	1.3	0.7	
	s.d.	0.2		0.3	0.2	0.4	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
August	1	2.9	19:35	2.2	1.7	1.1	01:45
1994	2	3.0	20:34	2.3	1.7	1.0	02:54
	3	3.0	21:26	2.4	1.7	0.9	03:46
	4	3.2	22:12	2.6	1.6	0.7	04:30
	5	3.3	22:55	2.7	1.6	0.7	05:07
	6	3.4	23:37	2.8	1.3	0.5	05:41
	7	3.0	12:37	3.0	1.2	0.4	06:15
	8	3.4	00:19	3.1	1.0	0.4	06:49
	9	3.4	01:03	3.2	0.9	0.4	07:23
	10	3.3	14:25	3.3	0.8	0.5	08:00
	11	3.4	15:07	3.1	0.8	0.7	08:40
	12	3.3	15:52	2.9	0.9	0.8	22:26
	13	3.3	16:45	2.7	1.1	0.8	23:33
	14	3.2	17:45	2.4	1.3	1.3	11:12
	15	3.2	18:54	2.4	1.4	0.7	00:48
	16	3.2	20:04	2.4	1.5	0.6	02:02
	17	3.3	21:09	2.5	1.4	0.5	03:09
	18	3.3	22:07	2.7	1.3	0.4	04:05
	19	3.4	22:59	2.9	1.2	0.4	04:53
	20	3.4	23:46	3.0	1.1	0.3	05:35
	21	3.1	12:32	3.1	1.0	0.4	06:14
	22	3.4	00:30	3.2	0.9	0.5	06:49
	23	3.3	01:11	3.2	0.9	0.6	07:22
	24	3.2	14:10	3.1	0.9	0.8	07:54
	25	3.1	14:42	3.0	1.0	1.0	21:03
	26	3.0	15:15	2.7	1.2	1.1	21:47
	27	3.0	15:51	2.6	1.4	1.2	22:37
	28	2.9	16:36	2.4	1.6	1.2	23:39
	29	2.8	17:33	2.3	1.7	1.7	11:08
	30	2.8	18:42	2.2	1.8	1.2	00:52
	31	2.8	19:52	2.3	1.8	1.1	02:02
	Highest	3.4		3.3	1.8	1.7	
	Lowest	2.8		2.2	0.8	0.3	
	Avg.	3.2		2.7	1.3	0.8	
	s.d.	0.2		0.3	0.3	0.3	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
November	1	3.5	10:05	3.1	1.0	0.5	16:36
1994	2	3.7	10:46	3.2	1.0	0.2	17:23
	3	3.8	11:29	3.8	1.0	0.1	05:18
	4	3.9	12:13	3.2	1.1	0.0	18:56
	5	3.9	12:59	3.2	1.2	0.0	19:44
	6	3.7	13:47	3.1	1.2	0.1	20:34
	7	3.5	14:39	3.1	1.4	0.3	21:27
	8	3.3	15:37	3.0	1.5	0.5	22:24
	9	3.0	16:44	2.9	1.6	0.8	23:26
	10	2.9	06:12	2.8	1.6	1.6	12:11
	11	3.0	07:15	2.7	1.4	1.0	00:31
	12	3.0	08:10	2.7	1.2	1.1	14:33
	13	3.1	08:57	2.7	1.2	1.1	15:27
	14	3.2	09:37	2.8	1.3	0.9	16:11
	15	3.3	10:12	2.9	1.3	0.7	16:50
	16	3.4	10:44	2.9	1.4	0.6	17:26
	17	3.4	11:16	3.4	1.5	0.6	18:01
	18	3.4	11:47	3.0	1.5	0.5	18:34
	19	3.4	12:19	2.9	1.6	0.5	19:07
	20	3.4	12:52	2.9	1.6	0.6	19:40
	21	3.3	13:27	2.9	1.7	0.7	20:14
	22	3.2	14:05	2.9	1.7	0.8	20:50
	23	3.1	14:47	2.8	1.7	0.9	21:30
	24	2.9	15:37	2.8	1.7	0.9	22:15
	25	2.9	05:05	2.8	1.7	1.1	23:06
	26	2.9	05:58	2.7	1.6	1.6	12:11
	27	3.0	06:52	2.6	1.3	1.2	00:05
	28	3.2	07:46	2.7	1.2	1.0	14:27
	29	3.4	08:37	2.8	1.2	0.7	15:24
	30	3.6	09:26	2.9	1.3	0.4	16:15
	Highest	3.9		3.8	1.7	1.6	
	Lowest	2.9		2.6	1.0	0.0	
	Avg.	3.3		2.9	1.4	0.7	
	s.d.	0.3		0.2	0.2	0.4	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
January	1	3.9	11:43	3.1	1.3	0.0	18:32
1995	2	3.8	12:32	3.2	1.2	0.0	19:16
	3	3.7	13:21	3.3	1.2	0.2	19:59
	4	3.5	14:10	3.3	1.2	0.4	20:42
	5	3.3	03:13	3.3	1.3	0.6	21:24
	6	3.2	03:58	3.0	1.3	0.9	22:06
	7	3.2	04:43	2.7	1.4	1.2	22:51
	8	3.1	05:31	2.5	1.4	1.4	23:39
	9	3.0	06:22	2.3	1.3	1.3	13:16
	10	3.0	07:16	2.3	1.6	1.2	14:23
	11	3.1	08:10	2.4	1.7	1.1	15:21
	12	3.1	09:01	2.6	1.8	0.9	16:09
	13	3.2	09:47	2.7	1.8	0.8	16:50
	14	3.3	10:28	2.8	1.7	0.7	17:27
	15	3.4	11:07	3.4	1.6	0.6	18:00
	16	3.5	11:44	2.9	1.6	0.5	18:30
	17	3.5	12:21	3.0	1.5	0.5	19:01
	18	3.4	12:59	3.1	1.4	0.5	19:31
	19	3.4	13:38	3.1	1.4	0.6	20:03
	20	3.2	14:21	3.2	1.3	0.7	20:38
	21	3.3	03:10	3.0	1.2	0.9	21:16
	22	3.3	03:51	2.8	1.2	1.0	21:16
	23	3.3	04:37	2.6	1.2	1.2	11:12
	24	3.3	05:32	2.4	1.4	1.0	12:25
	25	3.3	06:34	2.4	0.9	0.9	13:41
	26	3.4	07:41	2.5	1.5	0.7	14:51
	27	3.5	08:46	2.7	1.6	0.5	15:51
	28	3.6	09:46	2.9	1.5	0.3	16:42
	29	3.7	10:40	3.0	1.4	0.2	17:29
	30	3.7	11:32	3.7	1.2	0.2	18:12
	31	3.7	12:20	3.2	1.1	0.2	18:53
	Highest	3.9		3.7	1.8	1.4	
	Lowest	3.0		2.3	0.9	0.0	
	Avg.	3.4		2.9	1.4	0.7	
	s.d.	0.2		0.4	0.2	0.4	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
February	1	3.6	13:10	3.3	1.1	0.3	19:37
1995	2	3.4	13:55	3.4	1.1	0.5	20:14
	3	3.4	02:38	3.2	1.1	0.8	20:50
	4	3.3	03:15	3.0	1.1	1.0	21:25
	5	3.2	03:53	2.7	1.3	1.2	10:15
	6	3.1	04:33	2.5	1.5	1.3	11:12
	7	3.0	05:19	2.3	1.7	1.3	12:19
	8	3.0	06:15	2.3	1.3	1.3	13:34
	9	2.9	07:19	2.3	1.8	1.2	14:43
	10	3.0	08:23	2.5	1.9	1.0	15:38
	11	3.1	09:18	2.6	1.8	0.9	16:22
	12	3.2	10:05	2.8	1.7	0.8	16:59
	13	3.3	10:47	2.9	1.6	0.6	17:32
	14	3.4	11:27	3.4	1.4	0.6	18:02
	15	3.4	12:06	3.1	1.3	0.5	18:33
	16	3.4	12:46	3.2	1.1	0.6	19:05
	17	3.4	13:28	3.3	1.0	0.6	19:38
	18	3.4	02:00	3.2	0.9	0.8	20:14
	19	3.4	02:38	3.0	0.9	0.9	08:55
	20	3.4	03:19	2.8	1.1	0.9	09:48
	21	3.4	04:07	2.6	1.3	0.9	10:50
	22	3.3	05:03	2.4	1.5	0.9	12:01
	23	3.2	06:10	2.4	0.8	0.8	13:20
	24	3.2	07:24	2.6	1.6	0.7	14:33
	25	3.3	08:37	2.7	1.6	0.6	15:35
	26	3.4	09:40	2.9	1.4	0.5	16:27
	27	3.5	10:36	3.1	1.2	0.4	17:12
	28	3.5	11:26	3.5	1.1	0.4	17:52
	Highest	3.6		3.5	1.9	1.3	
	Lowest	2.9		2.3	0.8	0.3	
	Avg.	3.3		2.9	1.3	0.8	
	s.d.	0.2		0.4	0.3	0.3	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
April	1	3.4	00:43	3.1	1.1	0.6	07:10
1995	2	3.4	01:19	3.0	1.2	0.7	07:46
	3	3.3	01:50	2.8	1.4	0.7	08:22
	4	3.2	02:22	2.7	1.5	0.8	09:00
	5	3.1	02:56	2.6	1.6	0.9	09:42
	6	3.0	03:36	2.5	1.8	1.1	10:30
	7	2.8	04:25	2.4	1.8	1.2	11:29
	8	2.7	05:27	2.5	1.2	1.2	12:35
	9	2.7	06:42	2.6	1.8	1.2	13:41
	10	2.7	21:09	2.7	1.7	1.1	14:36
	11	2.9	09:01	2.8	1.5	1.0	15:23
	12	3.1	22:24	2.9	1.2	0.9	16:05
	13	3.4	23:00	3.0	0.9	0.9	04:39
	14	3.5	23:38	3.1	0.9	0.6	05:22
	15	3.2	12:21	3.2	0.9	0.4	06:05
	16	3.7	00:17	3.2	1.0	0.2	06:50
	17	3.7	00:58	3.1	1.1	0.1	07:36
	18	3.7	01:42	2.9	1.2	0.2	08:24
	19	3.6	02:30	2.9	1.3	0.2	09:16
	20	3.4	03:23	2.8	1.5	0.4	10:13
	21	3.2	04:24	2.7	1.5	0.6	11:16
	22	3.0	05:36	2.8	0.7	0.7	12:25
	23	2.9	20:13	2.8	1.5	0.8	13:33
	24	3.0	21:06	2.8	1.3	0.9	14:35
	25	3.1	21:50	2.8	1.1	0.9	15:28
	26	3.2	22:29	2.9	1.0	0.9	04:10
	27	3.3	23:03	2.9	1.0	0.8	04:54
	28	3.3	23:36	3.0	1.1	0.6	05:33
	29	2.9	18:05	2.9	1.2	0.5	06:10
	30	3.4	00:07	2.9	1.3	0.5	00:07
	Highest	3.7		3.2	1.8	1.2	
	Lowest	2.7		2.4	0.7	0.1	
	Avg.	3.2		2.8	1.3	0.7	
	s.d.	0.3		0.2	0.3	0.3	

(continued)

TABLE B.3. (continued)

Month	Date	HHW		LHW	HLW	LLW	
July	1	3.2	01:42	2.9	1.4	0.6	08:21
1995	2	3.0	10:00	2.9	1.4	0.6	08:54
	3	3.0	16:06	2.9	1.3	0.8	09:30
	4	3.0	16:49	2.7	1.2	0.9	10:11
	5	3.0	17:38	2.6	1.0	1.0	10:57
	6	3.1	18:33	2.4	1.2	1.1	00:13
	7	3.2	19:32	2.4	1.3	0.9	01:23
	8	3.4	20:31	2.4	1.3	0.7	02:31
	9	3.5	21:28	2.6	1.3	0.4	03:32
	10	3.6	22:23	2.7	1.3	0.2	04:27
	11	3.7	23:16	2.9	1.2	0.0	05:18
	12	3.0	12:32	3.0	1.1	-0.1	06:05
	13	3.7	00:08	3.1	1.0	-0.1	06:51
	14	3.7	00:59	3.2	1.0	0.0	07:36
	15	3.5	01:50	3.2	1.0	0.2	08:20
	16	3.3	02:42	3.2	1.0	0.4	09:04
	17	3.1	03:35	3.0	1.1	0.7	09:48
	18	3.1	17:07	2.7	1.1	0.9	10:33
	19	3.0	17:57	2.5	1.2	1.2	11:22
	20	3.0	18:51	2.3	1.4	1.1	00:44
	21	2.9	19:47	2.3	1.5	1.1	01:51
	22	3.0	20:41	2.3	1.6	1.0	02:53
	23	3.0	21:30	2.4	1.6	0.9	03:46
	24	3.1	22:15	2.5	1.6	0.7	04:31
	25	3.2	22:55	2.6	1.5	0.6	05:10
	26	3.3	23:33	2.7	1.4	0.5	05:45
	27	2.8	12:41	2.8	1.4	0.5	06:17
	28	3.3	00:11	2.9	1.3	0.5	06:47
	29	3.3	00:48	3.0	1.2	0.5	07:17
	30	3.2	01:26	3.0	1.2	0.6	07:47
	31	3.1	14:46	3.1	1.1	0.7	08:19
	Highest	3.7		3.2	1.6	1.2	
	Lowest	2.8		2.3	1.0	-0.1	
	Avg.	3.2		2.7	1.3	0.6	
	s.d.	0.2		0.3	0.2	0.4	

TABLE B.4. Tide conditions at Friday Harbor, Washington. Values (in meters) are corrected for Friday Harbor Laboratories for February, 1995. HHW = Highest, High Water; LHW = Lower, High Water; HLW = Higher, Low Water; LLW = Lowest, Low Water. Time of highest and lowest daily tide also indicated from tide tables. Source: University of Washington Friday Harbor Marine Laboratory.

Date	HHW		LHW	HLW	LLW		
Feb.1	2.7	17:23	2.2	1.3	0.0	23:59	
2	2.7	18:59	2.1	1.1	0.3	11:53	
3	2.6	19:17	1.9	1.0	1.0	13:43	
4	2.5	20:21	1.8	0.8	0.6	01:13	
5	2.5	21:38	1.7	0.9	0.7	03:26	
6	2.4	23:24	1.7	1.2	0.6	15:26	
7	2.4	09:31	2.4	1.5	0.5	17:17	
8	2.3	00:20	1.8	1.7	0.4	18:12	
9	2.2	11:20	2.0	1.8	0.3	19:03	
10	2.2	11:43	2.2	1.9	0.2	19:48	
11	2.3	12:42	2.2	1.8	0.1	20:33	
12	2.3	04:25	2.1	1.8	0.0	21:12	
13	2.4	04:49	2.1	1.7	0.0	21:48	
14	2.4	05:12	2.1	1.5	0.0	22:23	
15	2.4	05:35	2.1	1.3	0.0	22:57	Full Moon
16	2.5	06:00	2.1	1.1	0.2	23:32	
17	2.5	06:26	2.0	1.0	0.4	11:17	
18	2.5	06:55	2.0	0.7	0.6	12:59	
19	2.5	07:24	1.9	0.5	0.5	13:45	
20	2.5	07:56	1.9	1.0	0.4	14:40	
21	2.5	08:31	1.9	1.3	0.3	15:37	
22	2.5	09:12	2.5	1.6	0.1	16:44	
23	2.4	10:02	2.0	1.8	0.0	17:50	
24	2.4	11:06	2.2	1.9	0.0	18:54	
25	2.4	02:49	2.3	1.8	0.0	19:52	
26	2.5	03:32	2.3	1.7	0.0	20:45	
27	2.5	04:09	2.3	1.5	0.0	21:34	
28	2.5	04:42	2.2	1.3	0.1	22:16	
Highest	2.7		2.5	1.9	1.0		
Lowest	2.2		1.7	0.5	0.0		
Avg.	2.4		2.1	1.4	0.3		
s.d.	0.1		0.2	0.4	0.3		

APPENDIX C: SUPPLEMENTAL DATA

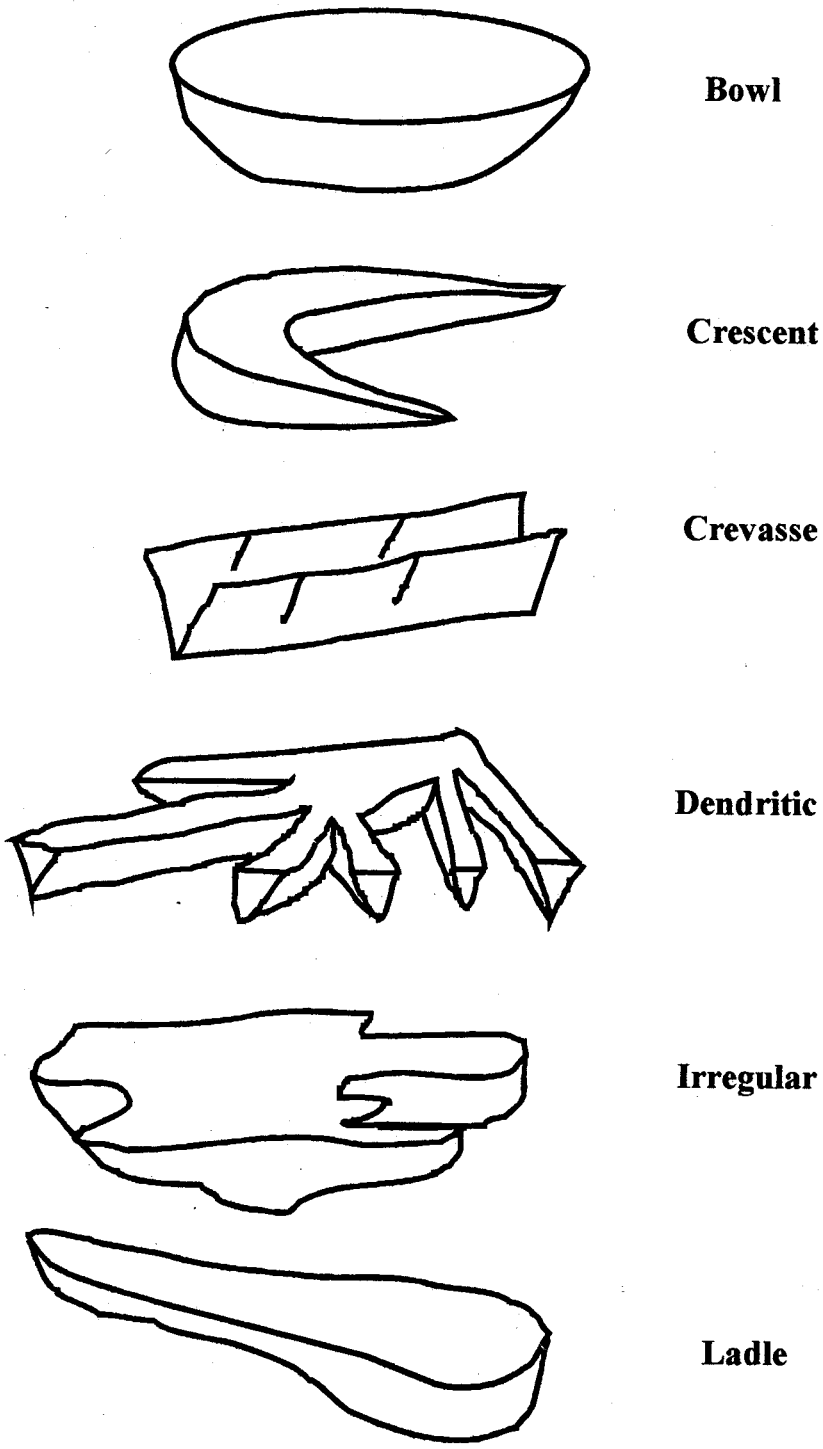

FIGURE C.1. Generalized splashpool basin types. Designations illustrate the categories of splashpool shape used for the descriptions of Table C.1. Note that in some instances, the basin 'type' may change according to the volume or depth of water contained within the basin, particularly on a heavily incised or jagged bedrock platform.

TABLE C.1. (*begins page over*). Summary of pool conditions. Season indicated per the sampling intervals of Figure B.1. Pool # indicates location (D = Diana Island; FB = First Beach; H = Helby Island; SB = Second Beach; W = Wizard Islet) and pool number from Figures A.1 to A.5. Elevation = tidal elevation of pool, in meters; Basin = Basin type, per Figure C.1; Windbreak = direction of predominate windbreak(s) or higher elevation relative to the pool; SA = pool surface area; Vol. = pool volume. Presence and census of *Tigriopus californicus* by generalized life-history stage based on the average result of replicate pipette samples. #/L = total number of *T. californicus* per liter sampled; #/pool = total individuals per liter extrapolated to the total pool volume. For brevity, the tabulated values represent the combined, averaged values for each pool in each season, however not all pools tabulated were sampled in each season. T.cal? = presence or absence of *T. californicus* during sampling; Male, Female = adult stages (C-IV to C-VI); Ovig. Fem. = ovigerous females; Cop'dite = stages C-I to C-IV, unidentified to gender; Nauplii = stages N-I to N-VI inclusive.

TABLE C.1. Summary of pool conditions. (Legend on previous page).

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Spring 1994	D 1	3.7	Dendritic	n/a	225	1125	n							
	D 2	2.9	Crescent	n/a	0.85	4.25	y	14.3	0	0	0	0	14.3	607.75
	D 3	3.7	Irregular	s	0.64	1.28	y	7.1	0	0	0	0	7.1	90.88
	D 4	5.2		se	2.5	5	n							
	D 5	5.1		s	0.75	2.25	n							
	D 6	3.5		n	2	12	n							
	D 7	5.2	Irregular	n,e,w,s	36	648	y	57.1	21.4	21.4	14.3	0	0	370008
	D 8	5.3	Crevasse	sw	0.65	1.3	y	35.6	7.1	7.1	0	7.1	14.3	462.8
	D 9	4.9	Irregular	w,e	3	12	y	49.9	14.3	7.1	7.1	7.1	14.3	5988
	D 10	3.8	Crevasse	nw,se	0.68	3.4	y	45	25	15	0	5	0	1530
	H 1	4.4	Dendritic	n,w	0.5	3	y	92.8	21.4	7.1	35.7	14.3	14.3	2784
	H 2	3.5	Crescent	sw	15	120	y	50	7.1	14.3	0	0	28.6	60000
	H 3	3.9	Crescent	n/a	0.5	2	n							
	H 4	4.5	Ladle	n,ne	15	75	y	14.3	0	0	14.3	0	0	10725
	H 5	3.8	Irreg./Den	e	0.75	3.75	n							
	H 6	2.5	Bowl	se	0.45	0.45	y	57.1	7.1	0	7.1	0	42.9	256.95
	H 7	2.7	Irregular	s	6	48	n							
	H 8	3.9	Ladle	s	0.5	10	n							
	H 9	5	Bowl, Ir	n	5	10	y	14.2	0	0	0	7.1	7.1	1420
	H 10	4.5	Irregular	n	0.5	3	y	42.8	0	0	21.4	14.3	7.1	1284
	H 11	4.1	Irregular	n	0.6	1.8	y	14.3	0	0	0	0	14.3	257.4
	H 12	3.3	Bowl	sw	0.8	4	y	21.4	0	0	0	0	21.4	856
	H 13	3.2	Irregular	n/a	0.1	0.4	y	7.1	0	0	0	0	7.1	28.4
	W 1	3.8	Irregular	nw,e	0.5	15	n							
	W 2	3.8	Irregular	ne	1.6	32	n							
	W 4	4	Irregular	nw	0.5	2.5	n							
	W 5	3.8	Crevasse	n,s	0.15	0.75	n							
	W 6	4.5	Irregular	s	2	16	y	7.1	0	0	0	7.1	0	1136
	W 7	3.8	Bowl	e,w	3	15	y	264.3	92.9	107.1	0	35.7	28.6	39645
	W 8	3.5	Irregular	sw	0.48	3.36	y	75	40	20	15	0	0	2520

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Spring 94	W 9	2.8	Irregular	n/a	1	0	y	42.8	7.1	28.6	7.1	0	0	0
(continued)	W 10	3.9	Irregular	n/a	4	100	y	35.7	0	7.1	14.3	14.3	0	35700
	W 11	3.9	Irregular	n/a	0.14	0	y	242.9	85.7	78.6	21.4	42.9	14.3	0
	W 12	2.5	Irregular	n/a	25	0	y	57	7.1	7.1	7.1	21.4	14.3	0
	W 13	3.5	Irregular	e	1	8	y	85.6	21.4	50	7.1	0	7.1	6848
	W 14	2.2	Bowl	n	12	840	y	85.7	21.4	42.9	7.1	0	14.3	719880
	W 15	3.9	Crevasse	e,w	10	50	y	57.1	21.4	14.3	0	21.4	0	28550
Summer 1994	D 1	3.4	Dendritic	n/a	50	300	n	0	0	0	0	0	0	0
	D 2	3.2	Irregular	n/a	0.42	2.1	y	66.6	33.3	33.3	0	0	0	1398.6
	D 3	3.7	Irregular	s	2.25	13.5	n							
	D 4	3.9	Crevasse	se	0	0	n							
	D 5	2.8	Bowl	se	0.189	1.13	n							
	D 6	4.4	Bowl	n	0.1925	1.35	y	898.5	397	307.7	123.1	70.8	0	12107.3
	D 7	5	Irregular	n,e,w,s	2	18	y	400	225	125	25	25	0	72000
	D 8	4.4	Crevasse	s,w	0.036	0.04	y	1280	656	432	96	96	0	460.8
	D 9	3.8	Irregular	w	0.84	3.36	y	480	190	160	53.3	76.7	0	16128
	D 10	3.7	Crevasse	ne,sw	0.4	1.2	y	500	220	240	40	0	0	6000
	D 11	4	Crevasse	n,s	5.5	49.5	y	200	100	75	25	0	0	99000
	FB 1	2.8	Bowl	n/a	0.7	2.1	y	250	125	75	0	50	0	5250
	FB 2	2.8	Irregular	n/a	6	30	y	250	125	100	25	0	0	75000
	FB 3	2.9	Bowl	n/a	6	120	y	585.7	317	162.9	80	25.7	0	702840
	FB 4	2.2	Bowl	n/a	2	100	y	150	50	0	0	100	0	150000
	FB 5	2.9	Irregular	n/a	4	20	y	100	0	0	0	100	0	20000
	FB 6	2.9	Irregular	n/a	1.5	7.5	y	1400	600	600	200	0	0	105000
	FB 7	2.9	Crevasse	n/a	1	6	n							
	FB 8	2.9	Irregular	n/a	1.17	4.68	y	250	125	125	0	0	0	11700
	FB 9	3.2		n/a		0	y	426.6	213	163.3	13.3	36.7	0	69322.5
	FB 10	2.3		n	3	18	y	133.3	100	33.3	0	0	0	23994
	FB 11	2.3		n/a	2.5	15	y	466.7	267	133.3	66.7	0	0	70005

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Summer 94	H 1	4.4	Dendritic	n,w	0.48	0.96	y	7.1	0	0	7.1	0	0	68.16
(continued)	H 2	3.5	Crescent	sw	0.135	0.41	y	21.3	7.1	7.1	0	7.1	0	86.27
	H 3	3.9	Crescent	n/a	0.21	1.26	n							
	H 4	4.1	Crevasse	n,sw	0.2	0.4	y	100	20	20	60	0	0	400
	H 5	3.8	Irreg./Den	e	1.1	3.3	y	220.1	86.7	86.7	26.7	6.7	13.3	7263.3
	H 6	2.5	Bowl	se	0.6	6	n							
	H 7	2.7	Irregular	s	3.5	35	n	0	0	0	0	0	0	0
	H 8	3.9	Ladle	s	1.05	21	n							
	H 9	5	Bowl, Irreg.	n	0.025	0.03	n							
	H 10	4.5	Irregular	n	0	0	n							
	H 11	4.1	Irregular	n	0.385	1.54	n							
	H 12	3.3	Bowl	sw	0.66	7.26	y	50	25	25	0	0	0	3630
	H 13	3.4	Irregular	n/a	0	0	y	133.4	66.7	66.7	0	0	0	0
	SB 1	3	Crevasse	e	10	420	y	433.4	267	100	66.7	0	0	1820280
	SB 2	3	Irregular	n	9	216	n							
	SB 3	4		s	2	36	y	300	150	125	25	0	0	108000
	SB 4	4	Irregular	s	24	720	n							
	SB 5	3.9	Crevasse	w	6.75	540	n							
	SB 6	4.5	Irregular	n	0.6	3	n							
	SB 7	3.8	Ladle	n/a	4	108	y	800	350	300	150	0	0	864000
	W 1	3.5	Irregular	s	1.6	25.6	y	21.4	0	0	0	0	21.4	5478.4
	W 2	2.8	Irregular	n	2	26	y	21.4	0	0	0	0	21.4	5564
	W 3	3.3	Ladle	s	1.2	9.6	n							
	W 4	4	Irregular	nw	2.4	28.8	y	42.9	0	0	0	0	42.9	12355.2
	W 5	3.8	Crevasse	n,s	1.2	10.8	n							
	W 6	4.5	Irregular	s	0.35	6.3	y	14.2	7.1	7.1	0	0	0	894.6
	W 7	3.8	Bowl	e,w	0.9	4.5	n							
	W 7	3.8	Bowl	e,w	12	240	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Summer 94	W 8	3.5	Irregular	sw	3	30	y	11.1	11.1	0	0	0	0	3330
(continued)	W 9	2.8	Irregular	n/a	1.6	8	y	14.3	0	0	0	0	14.3	1144
	W 10	3.9	Irregular	n/a	1.6	6.4	n							
	W 11	3.9	Irregular	n/a	0.6	2.4	y	14.2	7.1	7.1	0	0	0	340.8
	W 12	2.5	Irregular	n/a	14	1120	y	28.5	21.4	7.1	0	0	0	319200
	W 13	3.5	Irregular	e		0	n							
	W 14	2.2	Bowl	n	2.5	10	y	10	0	0	0	5	5	1000
	W 15	3.9	Crevasse	e,w	0	0	n							
Autumn 1994	D 1	3.4	Dendritic	n/a	2.8	16.8	y	766.7	300	100	200	100	66.7	128806
	D 2	3.2	Irregular	n/a	0.55	2.75	y	1135	345	280	185	310	15	31212.5
	D 3	3.7	Irregular	s	1.6	16	y	275	125	50	0	75	25	44000
	D 4	3.9	Crevasse	se	0.595	1.79	n							
	D 5	2.8	Bowl	se	0.2	0.6	n							
	D 6	4.4	Bowl	n	0.24	1.44	n							
	D 7	5	Irregular	n,e,w,s	30	600	n							
	D 8	4.4	Crevasse	s,w	1.75	8.75	y							
	D 9	3.8	Irregular	w	0.825	6.6	y	150	50	66.7	33.3	0	0	9900
	D 11	4	Crevasse	n,s	17.1	205.2	n							
	D 12	3.2	Bowl	s	5	50	n							
	D 13	5.5	Irregular	s,e	0.56	3.36	n							
	D 14	3.2	Crevasse	s,e	0.225	2.03	n							
	D 15	6.7	Dendritic	w,e	4.2	33.6	y	200	75	100	25	0	0	67200
	D 16	6.7	Dendritic	w,e	1.2	6	y	175	100	50	25	0	0	10500
	D 17	3.9	Crevasse	n,s	0.09	0.54	y	475	150	225	75	25	0	2565
	D 18	4.6	Irregular	n,s	1.05	13.65	y	583.4	292	175	16.7	50	50	79634.1
	D 19	5.4	Irregular	n	0.4	2.8	y	150	50	50	25	25	0	4200
	D 20	4.8	Crevasse	n,s	1	20	y	160	40	40	40	40	0	32000
	FB 1	2.8	Bowl	n/a	0.56	2.8	y	200.1	66.7	66.7	0	66.7	0	5602.8

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Autumn 94	FB 3	2.9	Bowl	n/a	12	420	y	150	0	50	0	100	0	630000
(continued)	FB 4	2.9	Bowl	sw	2.8	182	y	60	20	40	0	0	0	109200
	FB 5	2.9	Irregular	n/a		0	n							
	FB 6	3.5	Irregular	n	1.43	8.58	y	600	260	140	80	120	0	51480
	FB 7	3.1	Crevasse	n/a	1.35	5.4	y	475	175	175	75	50	0	25650
	FB 8	2.9	Irregular	ne	1.2	4.8	n							
	FB 9	3.2	Irregular	n/a	2.2	19.8	n							
	FB 10	3.2	Dendritic	nw	2.8	14	y	300	100	125	0	75	0	42000
	FB 11	3.2	Dendritic	ne	10.8	97.2	y	375	150	175	50	0	0	364500
	FB 12	2.6	Irregular	n/a	0.28	0.84	n							
	FB 13	2.6	Irregular	n/a	0.98	1.96	y							
	FB 14	2.6	Irregular	n/a	0.28	0.84	n							
	FB 15	2.2	Irregular	s	2	6	y	283.4	117	116.7	0	50	0	17004
	H 1	4.4	Dendritic	n,w	3.85	26.95	n							
	H 2	3.5	Crescent	sw	3.6	61.2	y	425	175	100	100	25	25	260100
	H 3	3.9	Crescent	n/a	2.25	18	n							
	H 4	4.1	Crevasse	n,sw	5.2	46.8	y	150	75	50	25	0	0	70200
	H 5	3.8	Irreg./Den	e	1.75	12.25	y	100	50	25	0	25	0	12250
	H 6	2.5	Bowl	se	0.98	7.84	y	100	50	25	0	25	0	7840
	H 7	2.7	Irregular	s	6	66	y	550	125	250	125	50	0	363000
	H 8	3.9	Ladle	s	1.05	18.9	n							
	H 9	5	Bowl, Ir	n	0.56	2.8	n							
	H 10	4.5	Irregular	n	1.76	17.6	n							
	H 11	4.1	Irregular	n	1.5	9	y	847.6	414	250	126.2	57.1	0	76284
	H 12	3.3	Bowl	sw	1.8	37.8	y	425	125	150	75	25	50	160650
	H 13	3.4	Irregular	n/a	2	16	n							
	H 14	5.2	Dendritic	n,e,w	2.5	12.5	n							
	H 15	4.7	Irregular	n,s	0.8	2.4	y	283.3	150	77.8	22.2	22.2	11.1	6799.2
	H 16	4.4	Irregular	n	1.5	18	n							
	H 17	4.7	Irregular	e,sw	2.5	40	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Autumn 94	H 18	4.7	Bowl	n,w	3	39	y	350	100	75	25	125	25	136500
(continued)	H 19	2.9	Bowl?	w	1.05	3.15	n							
	H 19	2.9	Bowl?	w	1.05	3.15	n							
	H 20	4.9	Dendritic	n/a	3.75	18.75	n							
	SB 1	2.9	Irregular	sw	12.5	687.5	y	350	75	150	50	75	0	2406250
	SB 2	2.9	Irregular	n	10.5	252	y	300	75	150	0	75	0	756000
	SB 3	4	Irregular	e,s	2.25	24.75	n							
	SB 4	2.8	Irregular	s	22.5	450	n							
	SB 5	3.1	Crevasse	w	6.75	540	y	125	50	25	50	0	0	675000
	SB 6	4.5	Irregular	ne	0.5	1.5	y	140	60	60	0	20	0	2100
	SB 8	3.3	Bowl	sw	0.21	0.63	y	80	40	40	0	0	0	504
	SB 9	4	Irregular	s	0.88	8.8	y	46.7	20	6.7	6.7	13.3	0	4109.6
	SB 10	3.1	Dendritic	s	1.56	14.04	n							
	SB 11	6	Bowl	n	0.72	4.32	y	200	75	100	0	25	0	8640
	SB 12	2.3	Bowl	w	0.24	0.48	n							
	W 1	3.8	Irregular	nw,e	8.75	306.25	y	180	80	60	0	40	0	551250
	W 2	3.8	Irregular	ne	7.5	112.5	y	275	75	125	0	75	0	309375
	W 3	3.9	Ladle	n	4.95	74.25	y	125	50	25	0	50	0	92812.5
	W 4	4	Irregular	nw	2.8	56	n							
	W 5	3.8	Crevasse	n,s	2.25	36	y	333.3	100	100	0	133.3	0	119988
	W 6	4.5	Irregular	s	1.08	32.4	y	399.9	133	200	33.3	33.3	0	129568
	W 7	3.8	Bowl	e,w	0.38	1.9	n							
	W 8	3.5	Irregular	sw	6	102	y	100	25	25	0	50	0	102000
	W 9	2.8	Irregular	n/a	1.43	11.44	n							
	W 10	3.9	Irregular	n/a	4.6	27.6	n							
	W 11	3.9	Irregular	n/a	10	50	y	536.4	300	172.7	18.2	45.5	0	268200
	W 12	2.5	Irregular	n/a	3.3	9.9	y	434.3	183	120	91.4	40	0	42995.7
	W 13	3.5	Irregular	e	1.47	2.94	y	384	172	124	84	4	0	11289.6

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Autumn 94	W 14	2.2	Bowl	n	1.35	4.05	y	240	160	60	20	0	0	9720
(continued)	W 15	3.9	Crevasse	e,w	1.44	2.88	y	175	100	50	25	0	0	5040
	W 16	3.9	Crevasse	sw	2.25	33.75	n							
	W 17	4.2	Crevasse	n,e	1.2	24	n							
	W 18	4.1	Crevasse	se	1.89	7.56	y	225	100	125	0	0	0	17010
Winter 1995	D 1	3.4	Dendritic	n/a	50	500	n							
	D 2	3.2	Irregular	n/a	0.28	1.4	n							
	D 3	3.7	Irregular	s	1.6	8	n							
	D 5	2.8	Bowl	se	0.2625	1.31	y	60	0	0	0	0	60	787.5
	D 6	4.4	Bowl	n	0.24	1.68	n							
	D 7	5	Irregular	n,e,w,s	42	546	n							
	D 8	4.4	Crevasse	s,w	3	21	n							
	D 9	3.8	Irregular	w	0.78	3.9	n							
	D 10	3.7	Crevasse	nw,se	0.81	5.67	y	33.4	16.7	16.7	0	0	0	1893.78
	D 11	4	Crevasse	n,s	23	230	n							
	D 12	3.2	Bowl	s	2.52	37.8	n							
	D 13	5.5	Irregular	s,e	0.595	2.98	n							
	D 14	3.2	Crevasse	s,e	1	10	n							
	D 15	6.7	Dendritic	w,e	40	240	y	33.4	16.7	16.7	0	0	0	80160
	D 16	6.7	Dendritic	w,e	2.1	21	n							
	D 17	3.9	Crevasse	n,s	0.063	0.19	n							
	D 18	4.6	Irregular	n,s	1.19	9.52	n							
	D 19	5.4	Irregular	n	0.27	1.08	n							
	D 20	4.8	Crevasse	n,s	2.7	32.4	n							
	FB 1	2.8	Bowl	n/a	1.08	5.4	n							
	FB 2	2.8	Irregular	n/a	1.8	5.4	n							
	FB 3	2.9	Bowl	n/a	12	540	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Winter 1995	FB 4	2.9	Bowl	sw	2	120	n							
(continued)	FB 5	2.9	Irregular	n/a	3.75	15	n							
	FB 6	3.5	Irregular	n	1.3	11.7	n							
	FB 7	3.1	Crevasse	n/a	1.08	5.4	n							
	FB 8	2.9	Irregular	ne	1.35	8.1	n							
	FB 9	3.2	Irregular	n/a	2	8	y	25	25	0	0	0	0	2000
	FB 10	3.2	Dendritic	nw	2.38	11.9	y	50	25	25	0	0	0	5950
	FB 11	3.2	Dendritic	ne	10.8	43.2	n							
	FB 12	2.6	Irregular	n/a	0.4	0.8	n							
	FB 13	2.6	Irregular	n/a	0.2	0.6	n							
	FB 14	2.6	Irregular	n/a	1.71	5.13	n							
	FB 15	1.5	Crevasse	s	1.2	2.4	n							
	H 1	4.4	Dendritic	n,w	3.36	6.72	y	466.7	66.7	83.3	133.3	116.7	66.7	31362.2
	H 2	3.5	Crescent	sw	4.2	46.2	n							
	H 3	3.9	Crescent	n/a	1	9	y	40	0	20	20	0	0	3600
	H 4	4.1	Crevasse	n,sw	3.15	28.35	y	366.7	100	116.7	50	66.7	33.3	103959
	H 5	3.8	Irreg./Den	e	1.68	11.76	n							
	H 6	2.5	Bowl	se	0.91	7.28	n							
	H 7	2.7	Irregular	s	6	60	n							
	H 8	3.9	Ladle	s	0.7	14	n							
	H 9	5	Bowl, Ir	n	0.48	3.84	y	60	20	0	40	0	0	2304
	H 10	4.5	Irregular	n	1.33	14.63	n							
	H 11	4.1	Irregular	n	0.91	2.73	n							
	H 12	3.3	Bowl	sw	1.95	19.5	n							
	H 13	3.8	Dendritic	n/a	3.5	17.5	n							
	H 14	5.2	Dendritic	n,e,w	3.36	16.8	n							
	H 15	4.7	Irregular	n,s	0.88	5.28	n							
	H 16	4.4	Irregular	n	1.26	6.3	y	100	25	0	75	0	0	6300

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Winter 1995	H 17	4.7	Irregular	e,sw	4.5	72	n							
(continued)	H 18	4.7	Bowl	n,w	1.7	13.6	n							
	H 19	2.9	Bowl?	w	1.12	10.08	y	175	100	75	0	0	0	17640
	H 20	4.9	Dendritic	e	3.64	21.84	y	100	20	20	20	40	0	21840
	SB 1	2.9	Irregular	sw	32	1600	n							
	SB 2	2.9	Irregular	n	16	480	n							
	SB 3	4	Irregular	e,s	2.2	26.4	n							
	SB 4	2.8	Irregular	s	30	450	n							
	SB 5	3.1	Crevasse	w	4	320	n							
	SB 6	4.5	Irregular	ne	0.88	3.52	y	80	40	20	20	0	0	2816
	SB 6	4.5	Irregular	ne	3.25	97.5	n							
	SB 8	3.3	Bowl	sw	0.72	1.44	n							
	SB 9	4	Irregular	s	0.845	6.76	n							
	SB 10	3.1	Dendritic	s	2.52	15.12	n							
	SB 11	6	Bowl	n	0.63	2.52	n							
	W 1	2.5	Irregular	ne	10.5	399	n							
	W 2	3.8	Irregular	ne	1.6	32	n							
	W 3	3.9	Ladle	n	2.4	48	n							
	W 4	4	Irregular	nw	7.5	172.5	n							
	W 5	3.8	Crevasse	n,s	2	18	n							
	W 6	4.5	Irregular	s	0.54	1.62	n							
	W 7	3.8	Bowl	e,w	1.25	46.25	n							
	W 8	3.5	Irregular	sw	2.76	69	n							
	W 9	2.8	Irregular	n/a	4.2	12.6	y	180	40	60	0	20	60	22680
	W 10	3.9	Irregular	n/a	1.98	11.88	y	2440	420	240	900	300	580	289872
	W 11	3.9	Irregular	n/a	14	84	y	25	0	0	25	0	0	21000
	W 12	2.5	Irregular	n/a	4.56	13.68	y	75	25	50	0	0	0	10260
	W 13	3.5	Irregular	e	1.1	2.2	y	1200	500	275	300	100	25	26400
	W 14	2.2	Bowl	n	0.39	1.95	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Winter 95	W 15	3.9	Crevasse	e,w	1.8	7.2	n							
(continued)	W 16	3.9	Crevasse	sw	3.5	28	n							
	W 17	4.2	Crevasse	n,e	0.81	28.35	n							
	W 18	4.1	Crevasse	se	1.26	6.3	n							
Spring 1995	D 1	3.4	Dendritic	n/a	10	40	n							
	D 2	3.2	Irregular	n/a	0.12	0.24	n							
	D 3	3.7	Irregular	s	2.25	13.5	n							
	D 4	3.9	Crevasse	se	0.012	0.01	y	9886	2943	1885.7	1714.3	2457.1	885.7	1186.28
	D 5	2.8	Bowl	se	0.1	0.3	y	350	50	50	50	100	100	1050
	D 6	4.4	Bowl	n	0.24	1.2	n							
	D 7	5	Irregular	n,e,w,s	16	144	y	3580	1640	1040	400	440	60	5155200
	D 8	4.4	Crevasse	s,w	2.4	16.8	y	266.7	66.7	66.7	33.3	66.7	33.3	44805.6
	D 9	3.8	Irregular	w	0.91	6.37	y	33.3	33.3	0	0	0	0	2121.21
	D 10	3.7	Crevasse	ne,sw	0.35	2.8	n							
	D 11	4	Crevasse	n,s	22.5	225	n							
	D 12	3.2	Bowl	s	1.7	22.1	n							
	D 13	5.5	Irregular	s,e	0.56	2.24	y	3150	1350	1000	450	350	0	70560
	D 14	3.2	Crevasse	s,e	0.2	1.4	y	150	0	0	150	0	0	2100
	D 15	6.7	Dendritic	w,e	17.5	87.5	n							
	D 16	6.7	Dendritic	w,e	12.5	125	y	33.3	33.3	0	0	0	0	41625
	D 17	3.9	Crevasse	n,s	0.28	0.84	y	133.4	0	0	0	66.7	66.7	1120.56
	D 18	4.6	Irregular	n,s	1.25	10	y	233.3	100	100	33.3	0	0	23330
	D 19	5.4	Irregular	n	0.27	1.62	y	566.7	167	166.7	0	100	133.3	9180.54
	D 20	4.8	Crevasse	n,s	0.68	6.12	n							
	FB 1	2.8	Bowl	n/a	5.29	158.7								
	FB 2	2.8	Bowl	n/a	2.25	123.75								

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Spring 95	FB 11	3.2	Dendritic	ne	13	78	y	1200	700	300	0	200	0	936000
(continued)	FB 12	2.6	Irregular	n/a	0.105	0.21	y	200	100	100	0	0	0	420
	FB 13	2.6	Irregular	n/a	0.42	0.42	y	800	400	300	100	0	0	3360
	FB 14	2.6	Irregular	n/a	0.98	2.94	n							
	FB 15	2.2	Irregular	s	0.28	0.56	n							
	H 1	4.4	Dendritic	n,w	3.15	9.45	y	1400	600	133.3	333.3	200	133.3	132291
	H 2	3.5	Crescent	sw	1.5	9	y	1267	533	200	316.7	200	16.7	114003
	H 3	3.9	Crescent	n/a	0.4	1.6	y	2200	500	800	300	300	300	35200
	H 4	4.1	Crevasse	n,sw	1	6	y	3300	800	900	400	800	400	198000
	H 5	3.8	Irreg./Den	e	0.56	1.12	y	1267	267	400	66.7	533.3	0	14187
	H 6	2.5	Bowl	se	0.5	3.5	y	450	150	100	50	0	150	15750
	H 7	2.7	Irregular	s	0.75	2.25	y	2886	914	771.4	142.9	942.9	114.3	64930.5
	H 8	3.9	Ladle	s	0.7	9.8	n							
	H 9	5	Bowl, Ir	n	0.35	1.75	y	333.4	200	66.7	66.7	0	0	5834.5
	H 10	4.5	Irregular	n	0.42	2.1	y	533.3	200	66.7	133.3	0	133.3	11199.3
	H 11	4.1	Irregular	n	0.225	0.68	y	533.4	133	66.7	66.7	200	66.7	3600.45
	H 12	3.3	Bowl	sw	0.66	10.56	n							
	H 13	3.4	Irregular	n/a	0	0	n							
	H 14	5.2	Dendritic	n,e,w	2.25	6.75	y	200	66.7	133.3	0	0	0	13500
	H 15	4.7	Irregular	n,s	0.132	0.4	y	100	50	50	0	0	0	396
	H 16	4.4	Irregular	n	0.0216	0.02	y	700	0	200	100	200	200	151.2
	H 17	4.7	Irregular	e,sw	0.24	0.96	y	2750	1350	650	600	150	0	26400
	H 18	4.7	Bowl	n,w	0.16	0.64	y	800	150	150	150	200	150	5120
	H 19	2.9	Bowl?	w	0.068	0.14	y	9300	1600	1200	1000	5000	500	12648
	H 20	4.9	Dendritic	n/a	2.7	8.1	y	700	150	100	150	200	100	56700
	SB 1	2.9	Irregular	sw	9	360	n							
	SB 2	2.9	Irregular	n	10.5	262.5	n							
	SB 3	4	Irregular	e,s	1.32	17.16	y	333.2	133	33.3	133.3	33.3	0	57177.1
	SB 4	2.8	Irregular	s	20	300	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Spring 95	SB 5	3.1	Crevasse	w	4	400	n							
(continued)	SB 6	4.5	Irregular	ne	0.35	1.05	n							
	SB 8	3.3	Bowl	sw	0.16	0.32	y	400	200	200	0	0	0	1280
	SB 9	4	Irregular	s	0.99	5.94	n							
	SB 10	3.1	Dendritic	s	0.06	0.18	y	966.6	433	266.7	233.3	33.3	0	1739.88
	SB 11	6	Bowl	n	0.009	0	y	400	400	0	0	0	0	18
Spring 95	W 1	3.8	Irregular	nw,e	2.8	56	n							
(continued)	W 2	3.8	Irregular	ne	3.6	36	n							
	W 3	3.9	Ladle	n	2.1	33.6	n							
	W 4	4	Irregular	nw	1.08	12.96	y	2160	880	640	160	400	80	279936
	W 5	3.8	Crevasse	n,s	0.63	5.04	y	3750	0	1700	1450	600	0	189000
	W 6	4.5	Irregular	s	0.42	0.42	y	1400	600	400	0	266.7	133.3	5880
	W 7	3.8	Bowl	e,w	0.243	4.13	y	200	0	100	0	100	0	8262
	W 8	3.5	Irregular	sw	3.24	35.64	n							
	W 9	2.8	Irregular	n/a	1.12	0	dried							
	W 10	3.9	Irregular	n/a	0.63	2.52	y	6800	2200	2800	1400	400	0	171360
	W 11	3.9	Irregular	n/a	3.41	20.46	y	1400	600	200	200	200	200	286440
	W 12	2.5	Irregular	n/a	0	0								
	W 13	3.5	Irregular	e	0	0	dried							
	W 14	2.2	Bowl	n	0.08	0.24								
	W 15	3.9	Crevasse	e,w	0	0								
	W 16	3.9	Crevasse	sw	0	0	dried							
	W 17	4.2	Crevasse	n,e	0.78	11.7	y	600	400	200	0	0	0	70200
	W 18	4.1	Crevasse	se	0.045	0.09	y	1800	850	450	250	150	100	1620
Summer 1995	D 1	3.4	Dendritic	w,n	2.1	23.1	n							
	D 2	3.2	Irregular	n/a	0.28	0.56	n							
	D 3	3.7	Irregular	e,w	1.4	7	y	650	350	300	0	0	0	45500

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Summer 95	D 4	3.9	Crevasse	e,w	0.195	0.59	n							
(continued)	D 5	2.8	Bowl	se	0.24	1.2	y	400	200	100	100	0	0	4800
	D 6	4.4	Bowl	n	0.24	2.88	n							
	D 7	5	Irregular	n,e,w,s	14.4	216	n							
	D 8	4.4	Crevasse	s,w	1.755	12.29	n							
	D 9	3.8	Irregular	w	0.77	3.08	y	50	50	0	0	0	0	1540
	D 10	3.7	Crevasse	ne,sw	0.36	2.52	y	400	150	250	0	0	0	10080
	D 11	4	Crevasse	n,s	31.5	252	y	300	200	100	0	0	0	756000
	D 12	3.2	Bowl	e,s	1.5	24	y	100	50	0	50	0	0	24000
	D 15	6.7	Dendritic	w,e	5.5	121	n							
	D 16	6.7	Dendritic	w,e	2.52	35.28	n							
	D 17	3.9	Crevasse	n,s	0.28	0.84	y	450	200	150	50	0	50	3780
	D 18	4.6	Irregular	n,s	1.08	11.88	y	400	150	50	200	0	0	47520
	D 19	5.4	Irregular	n	0.15	0.75	n							
	D 20	4.8	Crevasse	n,s	0.42	1.68	y	300	50	0	150	50	50	5040
	FB 1	2.8	Bowl	n/a	5.75	11.5	y	1800	650	700	150	150	150	207000
	FB 2	2.8	Bowl	n/a	12.25	24.5	y	300	100	150	50	0	0	73500
	FB 3	2.9	Bowl	n/a	9.6	288	y	150	100	50	0	0	0	432000
	FB 4	2.9	Bowl	sw	2.34	117	n							
	FB 6	3.5	Irregular	n	0.54	2.16	y	950	500	250	50	0	150	20520
	FB 7	3.1	Crevasse	n/a	0.3	0.6	y	450	250	200	0	0	0	2700
	FB 8	2.9	Irregular	ne	0.84	1.68	y	350	250	100	0	0	0	5880
	FB 9	3.2	Irregular	n/a	0.78	2.34	y	350	150	50	0	50	100	8190
	FB 10	3.2	Dendritic	nw	0.32	0.64	y	7850	2600	1650	2900	450	250	50240
	FB 11	3.2	Dendritic	ne	4.4	13.2	y	1800	800	550	400	50	0	237600
	FB 16	3.2	Irregular	n/a	4.55	13.65	y	900	500	200	100	0	100	122850
	H 1	4.4	Dendritic	n,w	3.38	10.14	n							
	H 2	3.5	Crescent	sw	1	11	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Summer 95	H 3	3.9	Crescent	n/a	0.48	2.4	n							
(continued)	H 4	4.1	Crevasse	n,sw	1.26	8.82	n							
	H 5	3.8	Irreg./Den	e	1.02	7.14	n							
	H 6	2.5	Bowl	se	0.4	3.2	n							
	H 7	2.7	Irregular	s	5.25	21	y	150	100	50	0	0	0	31500
	H 8	3.9	Ladle	s	0.65	11.7	n							
	H 9	5	Bowl, Ir	n	0.28	0.84	n							
	H 10	4.5	Irregular	n	0.84	5.04	n							
	H 11	4.1	Irregular	n	0.84	5.04	n							
	H 12	3.3	Bowl	sw	0.88	10.56	y	1250	650	400	200	0	0	132000
	H 14	5.2	Dendritic	n,e,w	1.47	5.88	n							
	H 18	4.7	Bowl	n,w	0.32	0.96	n							
	H 19	2.9	Bowl?	w	0.06	0.12	n							
	H 20	4.9	Dendritic	n/a	2	6	n							
	SB 1	2.9	Irregular	sw	9.6	384	n							
	SB 2	2.9	Irregular	n	10.15	253.75	n							
	SB 3	4	Irregular	e,s	1.32	15.84	y	650	200	200	200	50	0	102960
	SB 4	2.8	Irregular	s	20	340	n							
	SB 5	3.1	Crevasse	w	3.51	386.1	n							
	SB 6	4.5	Irregular	ne	0.24	0.24	n							
	SB 7	3	Ladle	ne	1.6	56	n							
	SB 8	3.3	Bowl	sw	0.2	0.4	y	1000	200	200	100	0	500	4000
	SB 9	4	Irregular	s	1.08	6.48	n							
	SB 10	3.1	Dendritic	s	0.06	0.24	y	1350	650	400	250	50	0	3240
	W 1	3.8	Irregular	nw,e	2.45	61.25	n							
	W 2	3.8	Irregular	ne	5.04	65.52	n							
	W 3	3.9	Ladle	n	3.69	29.52	n							

(continued)

TABLE C.1. (continued)

Season	Pool #	Elev.(m)	Basin	Windbreak	SA (m^2)	Vol. (L)	T. cal.?	#/L	Male	Female	Ovig.Fem.	Cop'dite	Nauplii	#/pool
Summer 95	W 5	3.8	Crevasse	n,s	1.28	12.8	y	100	50	50	0	0	0	12800
(continued)	W 6	4.5	Irregular	s	0.3	0.6	y	400	200	200	0	0	0	2400
	W 7	3.8	Bowl	e,w	0.315	6.62	y	1700	950	500	200	50	0	112455
	W 9	2.8	Irregular	n/a	0.35	0.7	n							
	W 10	3.9	Irregular	n/a	1.12	5.6	y	0	0	0	0	0	0	0
	W 11	3.9	Irregular	n/a	3.78	26.46	y	550	150	100	100	150	50	145530
	W 13	3.5	Irregular	e	2.16	2.16	n							
	W 14	2.2	Bowl	n	0.12	0.12	n							
	W 17	4.2	Crevasse	n,e	0.72	10.8	y	1050	150	400	150	50	300	113400
	W 18	4.1	Crevasse	se	2.64	31.68	n							

TABLE C.2. Summary of avian specimens examined. All specimens were examined in October and November, 1995, at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. All specimens were in the form of dried skins stretched over a cotton body form. Prior to *ca.* 1960, skins were typically poisoned with arsenic (P. Auger, pers. comm.); specimens are also sometimes washed in Ivory Snow ® or a similar detergent, then wrapped in sawdust. However, the precise preparation method used for most specimens was not specified.

SPECIMEN	NMNH TAG #	COLLECTION	REMARKS
Genus *Haemotopus*			
H. bachmani male	157982 USDA Biol. Survey	1897 Granville, WA	
H. bachmani male	166799 USDA Biol. Survey	June 24, 1900 British Columbia	
H. bachmani male	366610 USDI Biol. Survey	May 16, 1936 Shunagin Island	
H. bachmani male	366612 USDI Biol. Survey	June 22, 1937 Little Kiska, Aleutian Islands	
H. bachmani male	157980 USDA Biol. Survey	June 21, 1897 Lapush, WA	
H. bachmani male	588899 USDI Biol. Survey	April 21, 1922	
H. bachmani male	157983 USDA Biol. Survey	September 15, 1897 Destruction Island	
H. bachmani female	61185 Smithsonian	March 8, 1959 Puget Sound, WA	
H. bachmani female	157984 USDA Biol. Survey	May 20, 1897	
H. bachmani female	414655 Smithsonian Coll'ns	August 13, 1909	
H. bachmani female	20337 USDA Biol. Survey	August 14, 1905 San Geronimo Island	
H. bachmani female	4625 Smithsonian	San Miguel Island, CA	
H. bachmani female	70650 Smithsonian	St. Martins Island, CA	
H. bachmani female	588900 USDI Biol. Survey	April 27, 1922 Cannon Beach, OR	

(continued)

TABLE C.2. (continued)

SPECIMEN	NMNH TAG #	COLLECTION	REMARKS
Genus *Larus*			
L. californicus male	573002 USDI Biol. Survey	November 15, 1974 Mather AFB, CA	Avitrol poisoning
L. californicus male	102867	November 24, 1884 Ventura, CA	
L. californicus male	183618 USDA Biol. Survey	September 15, 1901 Mono Lake, CA	
L. californicus male	203352 USDA Biol. Survey	February 14, 1906 Lapaz Bay, Mexico	
L. californicus male	589438 USDA Biol. Survey	September 3, 1933 Multnoma Island, OR	Unidentified crustacea
L. californicus male	261469 USDA Biol. Survey	October 7, 1915 Lake Bowdoin, MT	
L. californicus male	582796	April 14, 1984 Mono Lake, CA	510 g Isopoda?
L. californicus male	168596	July 13, 1901 Great Slave Lake	
L. californicus male	236797	February 20, 1915 Wilmington, CA	
L. californicus female	4509 USNM	(no date) Shoalwater Bay, WA	specimen in very good condition
L. californicus female	557578	August 22, 1982 Samoa Peninsula, CA	
L. californicus female	197421 USNM	December 15, 1985 Humbolt Bay, CA	
L. californicus female	589437	December 12, 1930 Gold Beach	
L. californicus female	158042 USDA Biol. Survey	September 20, 1897 Oyhut, WA	
L. californicus female	582804	April 30, 1984 Mono Co., CA	
L. californicus female	206156 USDA Biol. Survey	November 5, 1908 Great Slave Lake	
L. californicus female	589434 USDI Biol. Survey	May 29, 1934 Clear Lake, CA	

TABLE C.3. Pearson Product Moment Correlation of *Tigriopus californicus* life-history stage vs. density, temperature, salinity, and tidal elevation. r = Pearson (rank) correlation coefficient; P = probability value; n = sample size; (not tested) denotes reciprocal of other pairwise comparisons. For pairwise comparisons with P values less than 0.05, positive or negative correlations are suggested by **bold** type and positive or negative r values, respectively. For pairwise values with a P value greater than 0.05, no significant correlation exists. Source: Jandel, 1994.

Nauplii vs.		**Adult Males**	**Adult Females**	**Ovigerous Female**	**Copepodites**
	r	0.0137	0.0132	0.0759	(not tested)
	P	0.7690	0.7772	0.1028	
	n	463	463	463	
		Density/L	**Temperature**	**Salinity**	**Elevation**
	r	0.0645	-0.0749	-0.0682	0.0605
	P	0.1660	0.1074	0.1426	0.1982
	n	463	463	463	454

Copepodites vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Nauplii**
	r	4.77 E -001	8.50 E -001	4.89 E -001	0.0302
	P	1.39 E -027	6.29 E -130	4.23 E -029	0.5177
	n	462	462	462	462
		Density/L	**Temperature**	**Salinity**	**Elevation**
	r	6.95 E -001	0.0373	0.0138	0.0630
	P	8.81 E -068	0.4238	0.7672	0.1807
	n	462	462	462	453

Ovigerous Females vs.		**Adult Males**	**Adult Females**	**Copepodites**	**Nauplii**
	r	**0.9800**	7.38 E -001	(not tested)	(not tested)
	P	**0.0000**	1.21 E -080		
	n	463	463		
		Density/L	**Temperature**	**Salinity**	**Elevation**
	r	9.54 E -001	-0.0002	-0.0168	0.0693
	P	8.47 E -244	0.9971	0.7178	0.1403
	n	463	463	463	454

(continued)

TABLE C.3. (continued)

Adult Females vs.		**Adult Males**	**Ovigerous Females**	**Copepodites**	**Nauplii**
	r	0.7680	(not tested)	(not tested)	(not tested)
	P	2.186 E -091			
	n	463			
		Density/L	**Temperature**	**Salinity**	**Elevation**
	r	0.8990	0.0424	0.0166	0.0253
	P	1.07 E -167	0.3628	0.7210	0.5911
	n	463	463	463	454
Adult Males vs.		**Adult Females**	**Ovigerous Females**	**Copepodites**	**Nauplii**
	r	(not tested)	(not tested)	(not tested)	(not tested)
	P				
	n				
		Density/L	**Temperature**	**Salinity**	**Elevation**
	r	9.60 E -001	0.0212	-0.0031	0.0494
	P	1.66 E-257	0.6487	0.9471	0.2940
	n	463	463	463	454
Density/L vs.		**Temperature**	**Salinity**	**Elevation**	
	r	0.0225	-0.0024	0.0539	
	P	0.6298	0.95889	0.2518	
	n	463	463	454	

TABLE C.4. Spearman Rank Order correlation of elevation, temperature, salinity, and population density vs. *Tigriopus californicus* life-history stage. *rs* = Spearman correlation coefficient; *P* = probability value; *n* = sample size; (not tested) denotes reciprocal of other pairwise comparisons. For pairwise comparisons with *P* values less than 0.05, positive or negative correlations are suggested by **bold** type and positive or negative *rs* values, respectively. For pairwise values with a *P* value greater than 0.05, no significant correlation exists. Source: Jandel, 1994.

Elevation vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Copepodites**
	rs	-0.0100	-0.0126	0.0882	-0.0353
	P	0.8312	0.7891	0.0605	0.4540
	n	454	454	454	453
		Nauplii	**Temperature**	**Salinity**	**Density/L**
	rs	-0.0129	**-0.1600**	**0.0970**	-0.0415
	P	0.7847	**0.0000**	**0.0389**	0.3780
	n	454	454	463	454

Temperature vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Copepodites**
	rs	0.0821	0.0576	0.0595	0.0472
	P	0.0778	0.2163	0.2011	0.3113
	n	463	463	463	463
		Nauplii	**Salinity**	**Density/L**	
	rs	-0.0253	**0.5000**	0.0846	
	P	0.5865	**0.0000**	0.0688	
	n	463	463	463	

Salinity vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Copepodites**
	rs	0.0625	0.0431	0.0493	-0.0093
	P	0.1792	0.3549	0.2897	0.8418
	n	463	463	463	462
		Nauplii	**Temperature**	**Density/L**	
	rs	**-0.1600**	(not tested)	0.0339	
	P	**0.0000**		0.4661	
	n	463		463	

(continued)

TABLE C.4. (continued)

Density/L vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Copepodites**
	rs	**0.9500**	**0.9200**	**0.7500**	**0.7100**
	P	**0.0000**	**0.0000**	**0.0000**	**0.0000**
	n	463	463	463	463
		Nauplii	**Temperature**	**Salinity**	
	rs	**0.2800**	(not tested)	(not tested)	
	P	**0.0000**			
	n	463			

Adult Males vs.		**Adult Females**	**Ovigerous Females**	**Copepodites**	**Nauplii**
	rs	**0.9400**	**0.7300**	(not tested)	(not tested)
	P	**0.0000**	**0.0000**		
	n	463	463		

Adult Females vs.		**Adult Males**	**Ovigerous Females**	**Copepodites**	**Nauplii**
	rs	(not tested)	**0.6900**	0.6600	**0.1183**
	P		**0.0000**	0.6000	**0.0109**
	n		463	462	463

TABLE C.5. Spearman Rank Order correlation of *Tigriopus californicus* life-history stage pairwise comparisons. *rs* = Spearman correlation coefficient; *P* = probability value; *n* = sample size; (not tested) denotes reciprocal of other pairwise comparisons. For pairwise comparisons with *P* values less than 0.05, positive or negative correlations are suggested by **bold** type and positive or negative *rs* values, respectively. For pairwise values with a *P* value greater than 0.05, no significant correlation exists. Source: Jandel, 1994.

Nauplii vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Copepodites**
	rs	**0.1233**	**0.1183**	**0.1471**	**0.2300**
	P	**0.0079**	**0.0109**	**0.0015**	**0.0000**
	n	463	463	463	462
		Density/L	**Elevation**		
	rs	**0.2800**	-0.0129		
	P	**0.0000**	0.7847		
	n	463	454		

Copepodites vs.		**Adult Males**	**Adult Females**	**Ovigerous Females**	**Nauplii**
	rs	**0.6500**	**0.6600**	**0.4900**	**0.2300**
	P	**0.0000**	**0.0000**	**0.0000**	**0.0000**
	n	462	462	462	462
		Nauplii	**Density/L**	**Pool Elevation**	
	rs	**0.2300**	**0.7100**	-0.0353	
	P	**0.0000**	**0.0000**	0.4540	
	n	462	462	453	

Ovigerous Females vs.		**Adult Males**	**Adult Females**	**Copepodites**	**Nauplii**
	rs	**0.7300**	**0.6900**	**0.4900**	(not tested)
	P	**0.0000**	**0.0000**	**0.0000**	
	n	463	463	462	
		Density/L	**Pool Elevation**		
	rs	**0.7500**	0.0882		
	P	**0.0000**	0.0605		
	n	454	454		

Females vs.		**Adult Males**	**Ovigerous Females**	**Density/L**	**Pool Elevation**
	rs	**0.9400**	(not tested)	**0.9200**	-0.0126
	P	**0.0000**		**0.0000**	0.7891
	n	463		463	454

TABLE C.6. Two-way Analysis of Variance of *Tigriopus californicus* abundance with season and site location. Given the incidence of zero values in the data set, copepod abundance was transformed by $\log_{10}+1$. Power of test at $\alpha = 0.05$ is 0.979 for season and 0.879 for location. NB: Abundance data failed tests for normality and homogeneity of variance ($p < 0.0001$ in both instances). Source: Jandel, 1994.

Source of Variance	**DF**	**SS**	**MS**
Season	4	33.0	8.25
Location	4	23.9	5.97
Residual	454	592.0	1.30
Total	462	651.5	1.41

Source of Variance	**F**	**P**
Season	6.32	<0.0001
Location	4.58	0.0012

Least square means for Season Group	**Mean**	**Std. Error**
Spring 1994	1.013	0.254
Summer 1994	0.691	0.255
Autumn 1994	1.015	0.256
Winter 1994	1.425	0.273
Winter 1995	0.887	0.276

Least square means for Location Group	**Mean**	**Std. Error**
Diana Island	1.015	0.256
First Beach	1.425	0.273
Helby Island	0.691	0.255
Second Beach	0.887	0.276
Wizard Islet	1.013	0.254

TABLE C.7. Student-Newman-Keuls multiple comparisons for seasonal *Tigriopus californicus* abundance. Source: Jandel, 1994.

Comparison	**Δ means**	**p**	**q**
Autumn vs. Winter	1.407	5	1.715
Autumn vs. Winter	0.697	4	6.795
Autumn vs. Spring	0.301	3	2.016
Autumn vs. Summer	0.198	2	2.106
Summer vs. Winter 1994	1.209	4	1.475
Summer vs. Winter 1995	0.498	3	5.089
Summer vs. Spring	0.102	2	0.692
Spring vs. Winter 1994	1.107	3	1.333
Spring vs. Winter 1995	0.396	2	2.588
Winter 1994 vs. Winter 1995	0.711	2	0.866
	P < 0.05		
Autumn vs. Winter 1994	No		
(remainder not tested)			

TABLE C.8. Student-Newman-Keuls multiple comparisons for locational *Tigriopus californicus* abundance. Source: Jandel, 1994.

Comparison	**Δ means**	**p**	**q**
First Beach vs. Helby Island	0.73347	5	5.9444
First Beach vs. Second Beach	0.53818	4	3.2633
First Beach vs. Wizard Islet	0.41148	3	3.3076
First Beach vs. Diana Island	0.40967	2	3.2777
Diana Island vs. Helby Island	0.3238	4	3.0436
Diana Island vs. Second Beach	0.1285	3	0.8365
Diana Island vs. Wizard Islet	0.00181	2	0.0170
Wizard Islet vs. Helby Islet	0.32199	3	3.0777
Wizard Islet vs. Second Beach	0.12669	2	0.8300
Second Beach vs. Helby Island	0.19530	2	1.2785
	P < 0.05		
First Beach vs. Helby Island	Yes		
First Beach vs. Second Beach	No		
Diana Island vs. Helby Island	No		
(remainder not tested)			

TABLE C.9. Temperature and salinity replicate measures. Triplicate measures for pool temperature (°C) and salinity (°/₀₀) readings for Barkley Sound pools in January, 1995. D = Diana Island; FB = First Beach; H = Helby Island; W = Wizard Islet.

	Rep 1		Rep 2		Rep 3		Avg		SD	
Pool	Temp	Salinity	Temp	Salinity	Temp	Salinity	Temp	Salinity	Temp	Salinity
D1	10	25.3	9	28.5	9	28.2	9.3	27.3	0.6	1.8
D10	9	30.7	9	27.1	9	30.0	9	29.3	0	1.9
D11	10	31.1	9	30.1	9	30.3	9.3	30.5	0.6	0.5
D12	9	27.6	8	26.1	8	29.5	8.3	27.7	0.6	1.7
D13	9	29.4	8	20.9	8	28.1	8.3	26.1	0.6	4.6
D14	10	29.0	8	28.5	9	27.7	9	28.4	1	0.7
D15	9	27.0	9	28.7	8	27.7	8.7	27.8	0.6	0.9
D16	9	27.0	9	27.4	8	28.9	8.7	27.8	0.6	1.0
D17	9	30.7	10	28.9	9	16.0	9.3	25.2	0.6	8.0
D18	10	32.0	9	29.8	9	28.4	9.3	30.1	0.6	1.8
D19	9	30.8	9	28.6	9	28.8	9	29.4	0	1.2
D2	9	25.2	8	12.5	8	12.0	8.3	16.6	0.6	7.5
D20	9	31.8	9	28.6	9	28.6	9	29.7	0	1.9
D3	9	23.9	8	25.0	8	27.7	8.3	25.5	0.6	2.0
D4	8	28.0	9	6.6	8	8.0	8.3	14.2	0.6	12.0
D5	9	24.0	9	23.2	9	25.0	9	24.1	0	0.9
D6	10	23.5	10	23.4	10	26.8	10	24.6	0	1.9
D7	8	30.8	10	30.4	9	29.4	9	30.2	1	0.7
D8	9	27.7	9	23.2	9	23.8	9	24.9	0	2.4
D9	9	31.6	10	29.9	9	30.0	9.3	30.5	0.6	1.0
FB1	14	29.5	10	28.8	12	28.3	12	28.9	2	0.6
FB10	10	29.8	9	27.4	10	24.5	9.7	27.2	0.6	2.7
FB11	9	30.9	10	28.4	10	29.2	9.7	29.5	0.6	1.3
FB12	9	27.3	12	26.5	14	24.2	11.7	26.0	2.5	1.6
FB13	10	28.9	10	27.0	14	26.9	11.3	27.6	2.3	1.1
FB14	14	28.2	9	28.6	10	26.4	11	27.7	2.6	1.2
FB15	12	28.2	8	28.3	9	28.3	9.7	28.3	2.1	0.1
FB2	11	29.1	9	29.2	12	26.1	10.7	28.1	1.5	1.8
FB3	12	29.7	12	28.9	12	29.6	12	29.4	0	0.4
FB4	11	30.4	9	29.8	14	28.9	11.3	29.7	2.5	0.8
FB5	9	29.8	9	29.6	9	29.4	9	29.6	0	0.2
FB6	9	29.5	9	28.9	10	29.1	9.3	29.2	0.6	0.3
FB7	11	29.3	9	29.2	9	28.4	9.7	29.0	1.2	0.5
FB8	10	29.2	9	28.4	10	29.4	9.7	29.0	0.6	0.5
FB9	9	29.7	9	28.6	9	28.1	9	28.8	0	0.8

(continued)

TABLE C.9. (continued)

	Rep 1		Rep 2		Rep 3		Avg		SD	
Pool	**Temp**	**Salinity**	**Temp**	**Salinity**	**Temp**	**Salinity**	**Temp**	**Salinity**	**Temp**	**Salinity**
H1	9	11.3	11	6.3	10	5.4	10	7.7	1	3.2
H10	10	16.6	11	13.4	9	13.7	10	14.6	1	1.8
H11	10	16.2	10	13.5	11	14.2	10.3	14.6	0.6	1.4
H12	8	16.9	11	12.6	10	13.2	9.7	14.2	1.5	2.3
H13	10	27.7	11	14.5	10	14.3	10.3	18.8	0.6	7.7
H14	10	16.5	9	7.6	11	6.5	10	10.2	1	5.5
H15	11	53.1	11	12.0	10	12.1	10.7	25.7	0.6	23.7
H16	11	27.5	10	11.2	10	11.7	10.3	16.8	0.6	9.3
H17	10	9.6	11	12.7	10	11.0	10.3	11.1	0.6	1.6
H18	11	4.8	10	3.1	10	2.5	10.3	3.5	0.6	1.2
H19	11	10.8	11	6.9	10	5.6	10.7	7.8	0.6	2.7
H2	10	19.6	11	6.5	11	5.5	10.7	10.5	0.6	7.9
H20	12	11.0	10	6.6	11	5.5	11	7.7	1	2.9
H3	10	10.2	10	5.9	11	5.4	10.3	7.2	0.6	2.6
H4	10	9.8	10	6.5	11	5.9	10.3	7.4	0.6	2.1
H5	11	9.7	11	5.8	11	5.9	11	7.1	0	2.2
H6	10	26.3	9	14.6	11	13.5	10	18.1	1	7.1
H7	7	25.4	11	12.4	10	12.9	9.3	16.9	2.1	7.4
H8	10	26.3	10	13.8	8	13.1	9.3	17.7	1.2	7.4
H9	10	16.2	11	13.3	10	13.4	10.3	14.3	0.6	1.7
W1	9	19.7	9	3.0	10	4.0	9.3	8.9	0.6	9.4
W10	9	12.6	9	13.5	10	14.7	9.3	13.6	0.6	1.1
W11	8	9.2	8	14.5	8	12.9	8	12.2	0	2.7
W12	9	12.8	9	13.9	8	14.8	8.7	13.8	0.6	1.0
W13	11	9.8	9	10.7	8	11.6	9.3	10.7	1.5	0.9
W14	9	6.3	9	7.8	9	7.8	9	7.3	0	0.9
W15	9	8.9	8	9.1	8	8.2	8.3	8.7	0.6	0.5
W16	10	18.3	9	3.3	8	4.8	9	8.8	1	8.3
W17	9	53.6	9	3.4	9	5.3	9	20.8	0	28.5
W18	10	3.6	10	3.9	9	6.3	9.7	4.6	0.6	1.5
W2	9	17.1	8	3.0	10	4.4	9	8.2	1	7.8
W3	10	3.6	10	3.6	8	6.6	9.3	4.6	1.2	1.7
W4	8	17.6	9	3.3	9	4.9	8.7	8.6	0.6	7.8
W5	10	24.1	9	3.6	8	5.6	9	11.1	1	11.3
W6	9	5.4	10	3.4	9	5.7	9.3	4.8	0.6	1.3
W7	9	6.9	9	3.5	9	5.8	9	5.4	0	1.7
W8	9	3.5	10	3.8	9	6.2	9.3	4.5	0.6	1.5
W9	9	12.6	9	17.3	9	18.4	9	16.1	0	3.1

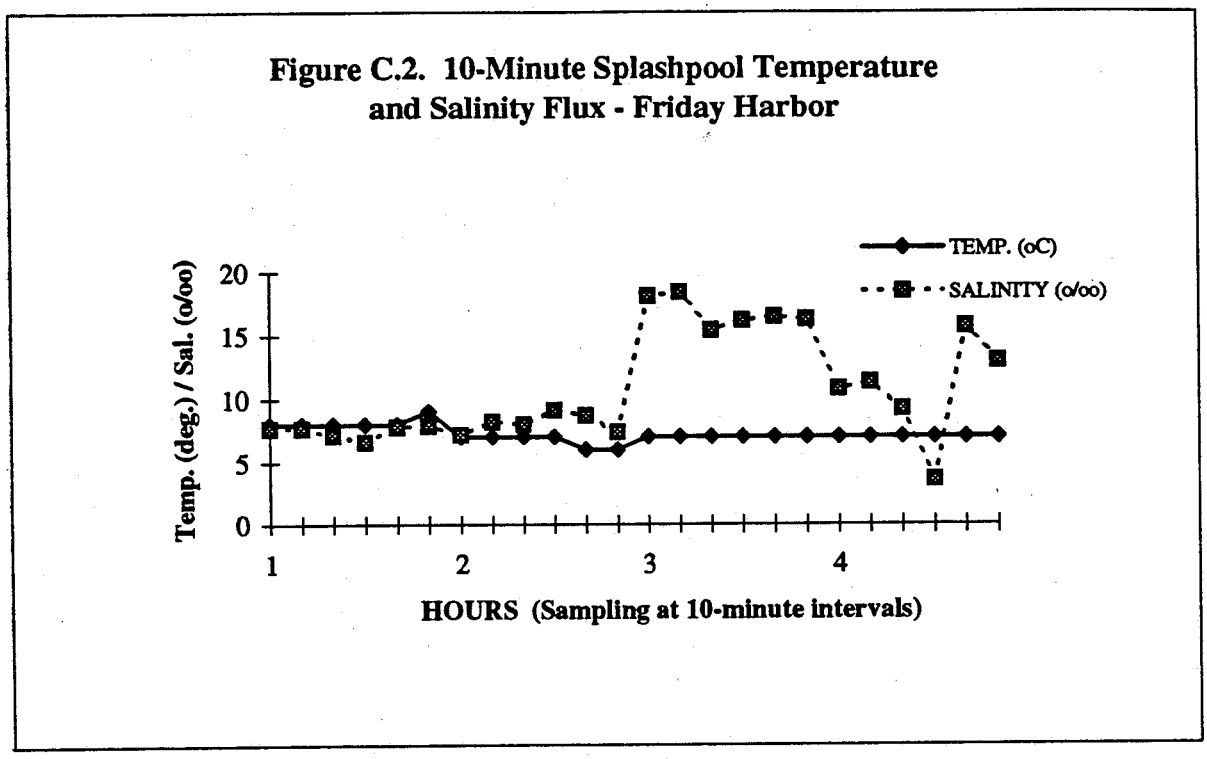

FIGURE C.2. Ten-minute splashpool temperature and salinity flux at Friday Harbor. Summary of temperature and salinity triplicate measurements taken each 10 minutes from one randomly selected pool at the Friday Harbor, Washington, study site (see Figure A.6) using the methods of Chapter 1. For clarity, error bars are not plotted.

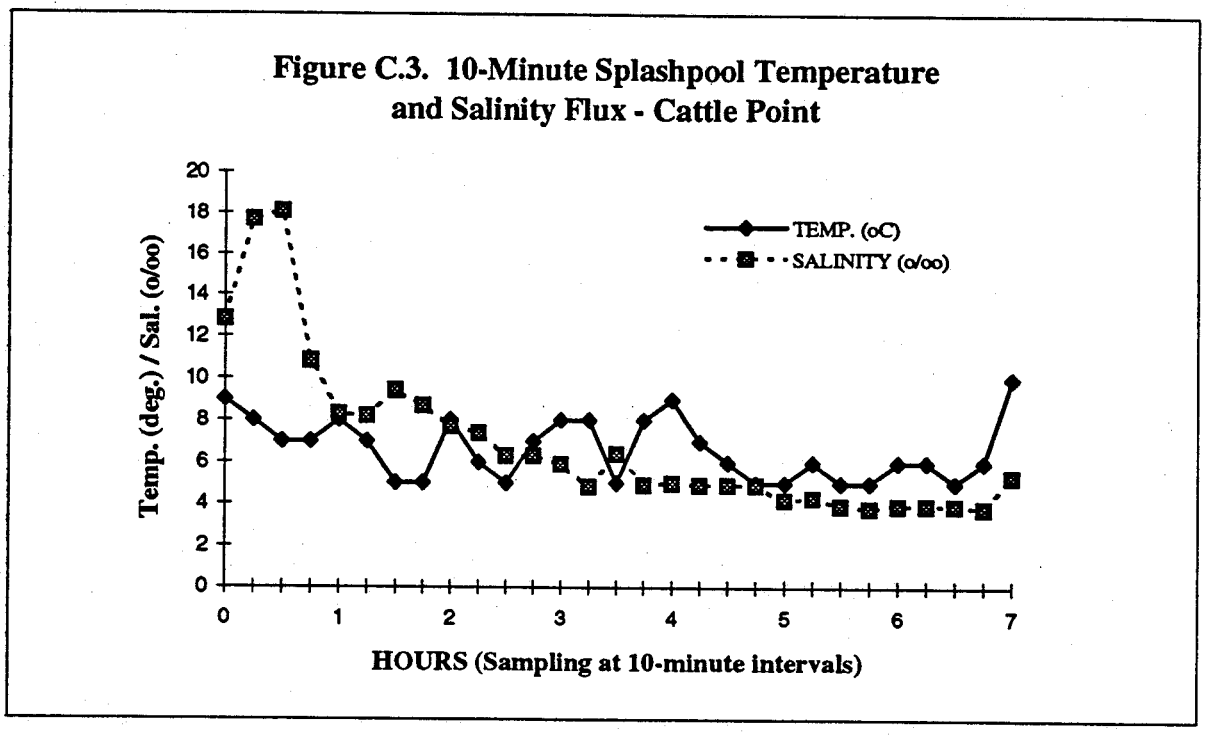

FIGURE C.3. Ten-minute splashpool temperature and salinity flux at Cattle Point. Summary of temperature and salinity triplicate measurements taken each 10 minutes from one randomly selected pool at the Cattle Point, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.

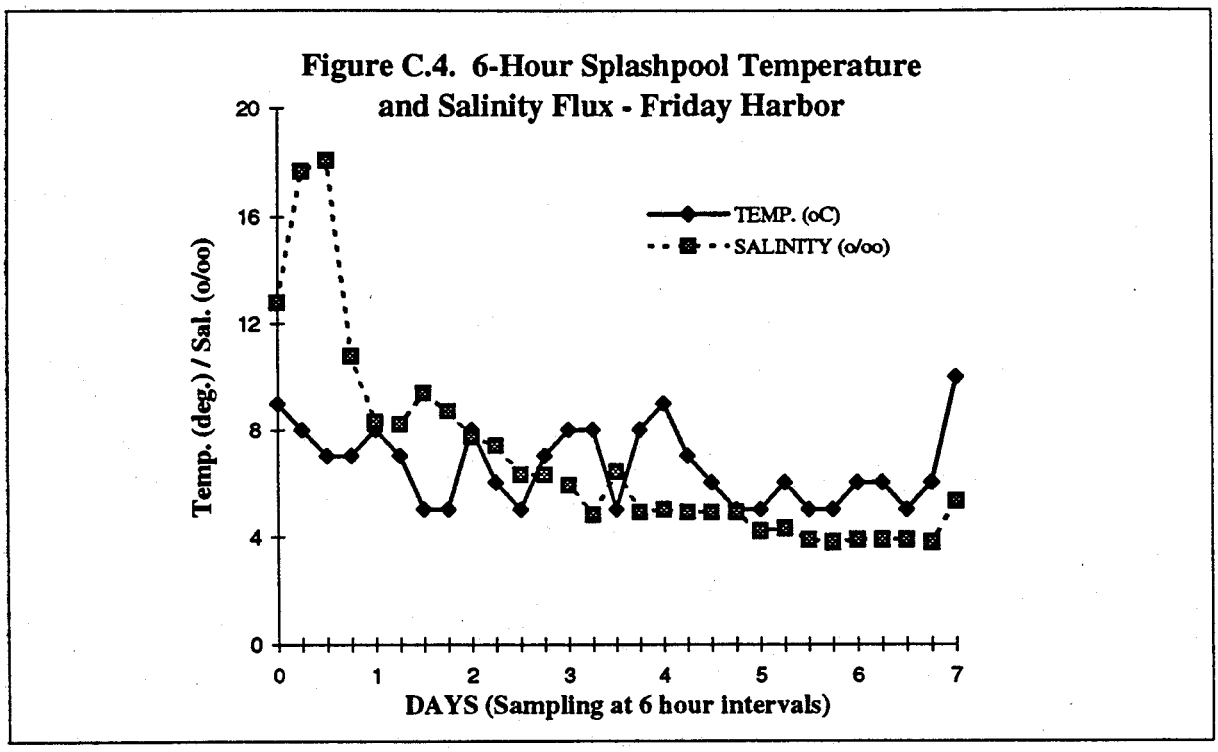

FIGURE C.4. Six-hour splashpool temperature and salinity flux at Friday Harbor. Summary of temperature and salinity triplicate measurements taken each 6 hours from one randomly selected pool at the Friday Harbor, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.

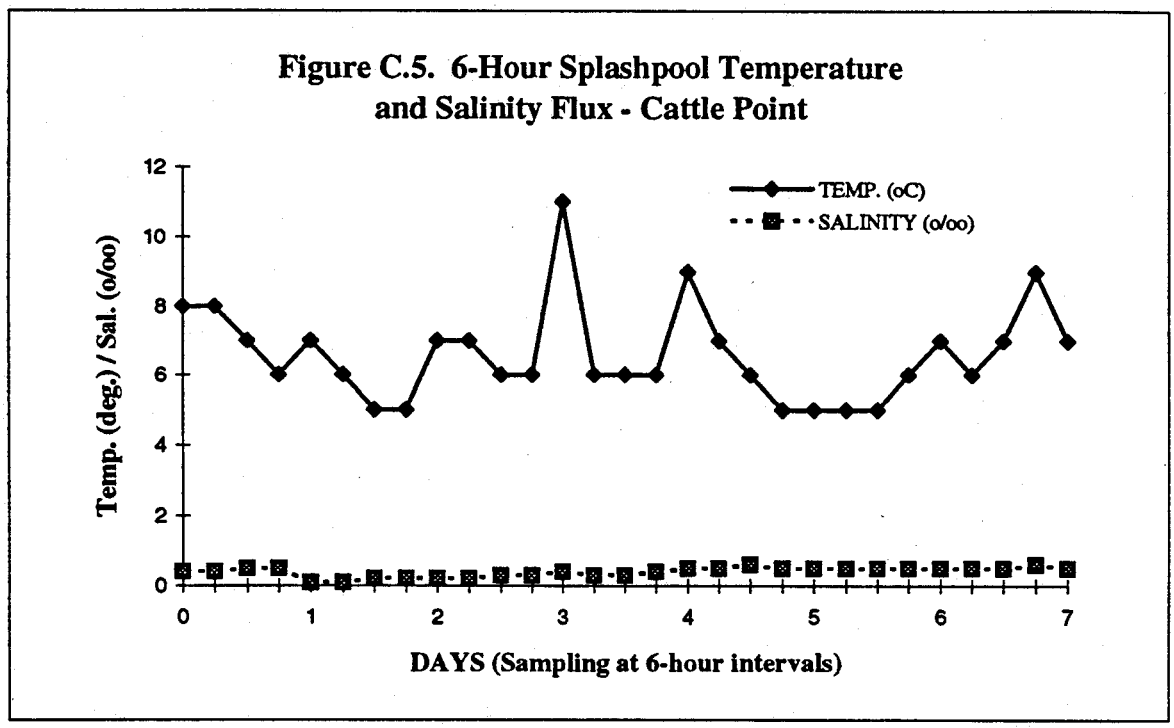

FIGURE C.5. Six-hour splashpool temperature and salinity flux at Cattle Point. Summary of temperature and salinity triplicate measurements taken each 6 hours from one, randomly selected pool at the Cattle Point, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.

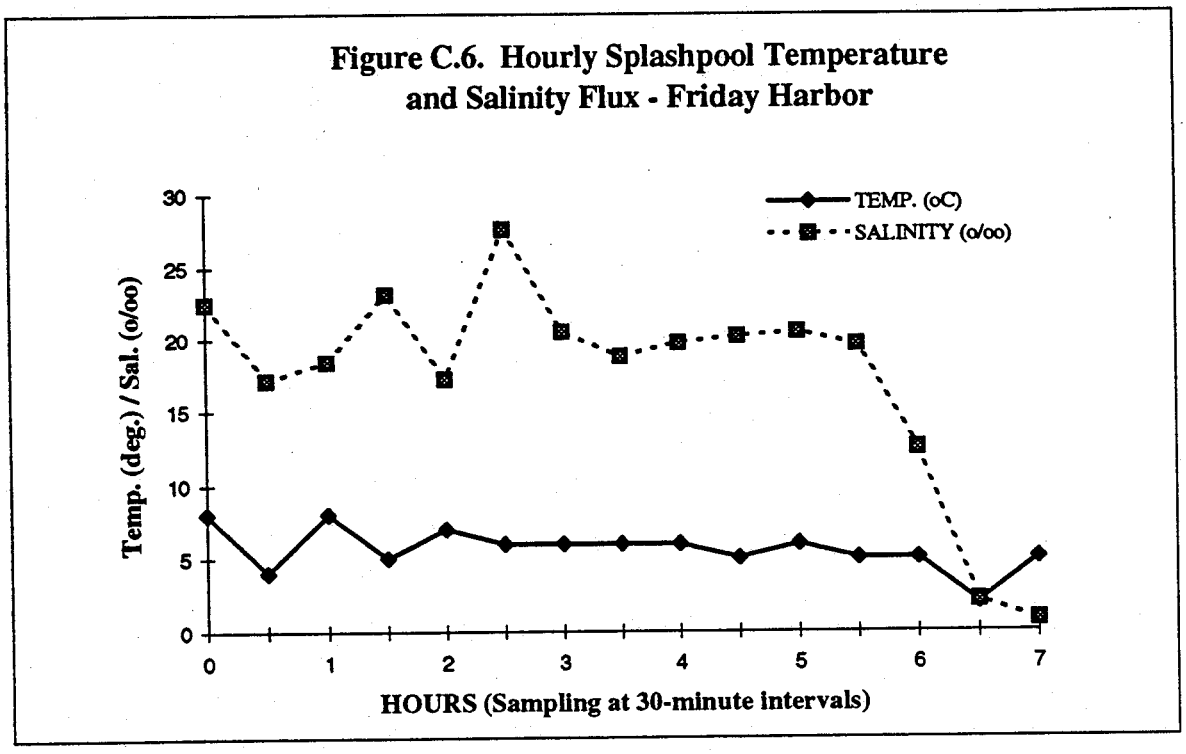

FIGURE C.6. Hourly splashpool temperature and salinity flux at Friday Harbor. Summary of temperature and salinity triplicate measurements taken each 30 minutes from one, randomly selected pool at the Friday Harbor, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.

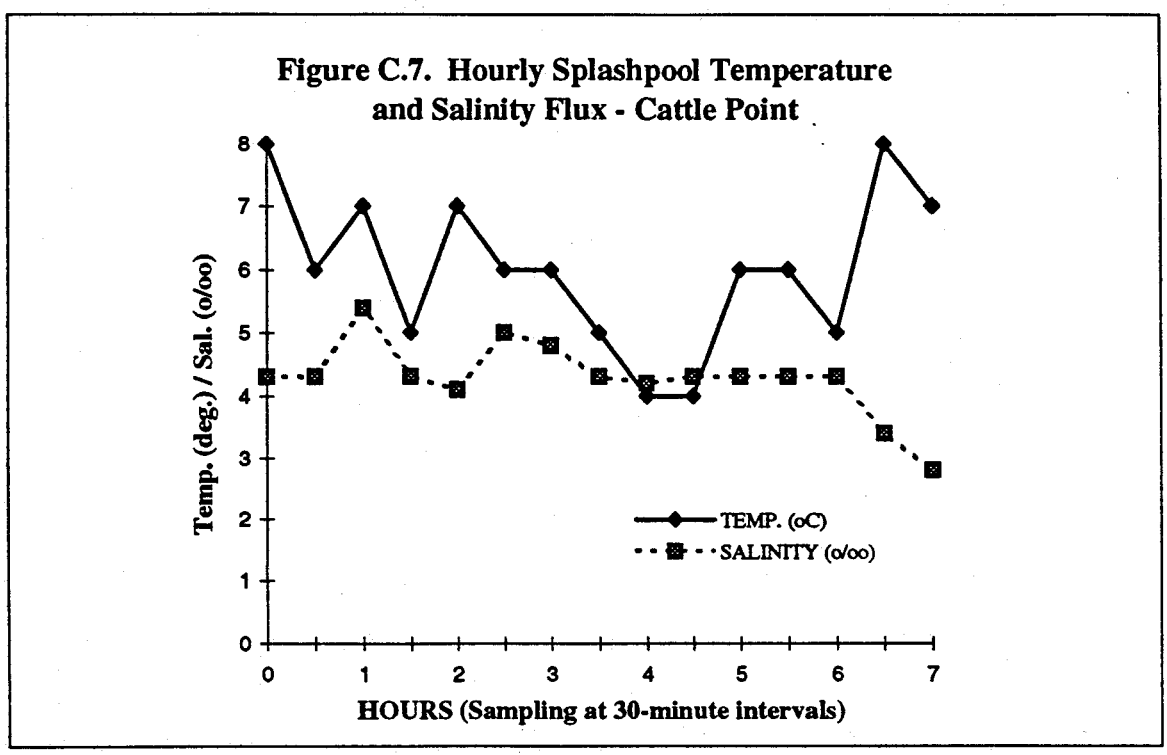

FIGURE C.7. Hourly splashpool temperature and salinity flux at Cattle Point. Summary of temperature and salinity triplicate measurements taken each 30 minutes from one, randomly selected pool at the Cattle Point, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.

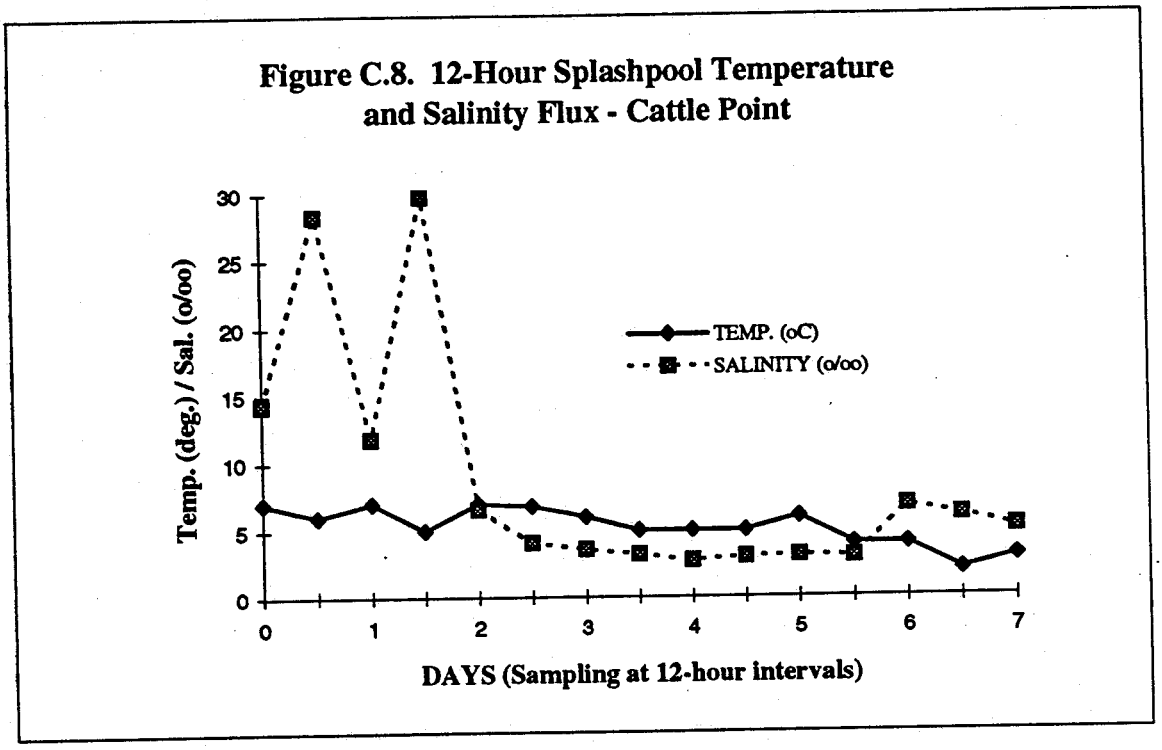

FIGURE C.8. Twelve-hour splashpool temperature and salinity flux at Cattle Point. Summary of temperature and salinity triplicate measurements taken each 12-hours from one, randomly selected pool at the Cattle Point, Washington, study site (see Figure A.6). For clarity, error bars are not plotted.