QUANTIFYING PREDATION ON PLANKTONIC LARVAL STAGES OF MARINE BENTHIC INVERTEBRATES

by

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For TH. Keep gleaming, Buddy!

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ABSTRACT

This thesis enhances our ability to develop hypotheses on effects of predation on the ecology of larval marine benthic invertebrates. I evaluated the mechanisms that influence encounter rates among predators and prey, and the potential impact of predation on larval abundance. I developed an individual-based model that facilitates the prediction of encounter rates between a motionless predator and prey that exhibit directional persistence (*i.e.,* the tendency to maintain direction of travel over time) in an isotropic random walk. Using data from simulations, I (1) showed that common assumptions of diffusive or ballistic prey movement results in overestimates of the rate of search for prey over relevant scales of prey perception and directional persistence; and (2) evaluated the utility of published analytical models for prediction of the rate of search at long time scales. In laboratory experiments, I showed that temperature influences the motility of different larval stages of the acorn barnacle, *Semibalanus balanoides*, by its effect on directional persistence and swimming speed, and that larval motility was anisotropic. In the field, I found that the potential impact of predation on larval barnacles by a ctenophore, *Pleurobrachia pileus*, was negligible, primarily due to large differences in the relative abundance of predator and prey. A review of studies that have quantified rates of predation on larval marine benthic invertebrates and fish indicate that predation is potentially ecologically significant in certain instances, but is not always detrimental to larval populations. Observations of ingestion, digestion, and egestion of larval barnacles in the pharynx of *P. pileus* in the laboratory indicated that the cypris stage may avoid mortality after ingestion, by resisting digestion and inducing egestion. Larvae probably face a gauntlet of predators over their pelagic duration. We need to identify these predators and quantify their potential impacts by developing mechanistic models of the "predation process", and making observations in the field. My thesis contributed observations to both of these objectives, and demonstrated methods (and their associated challenges) that can be used to quantify rates of search, ingestion, and prey mortality.

LIST OF ABBREVIATIONS AND SYMBOLS USED

Abbreviation or symbol	Description	Units
b	Scaling exponent in gut evacuation model	–
Bb	*Balanus balanus*	–
Bc	*Balanus crenatus*	–
C	Density of individuals	number m^{-3}
CRW	Correlated random walk	–
Cyp	Cypris Stage	–
d	Radial distance	m
df	degrees of freedom	–
D	Diffusivity	m^2 s^{-1}
2D	Two dimensions	–
3D	Three dimensions	–
e	Per-capita encounter rate	number s^{-1}
E	Encounter rate	encounters m^{-3} s^{-1}
Expt	Experiment	–
ESD	Equivalent spherical diameter	m
F	Clearance rate	m^{-3} s^{-1}
G	Gut content	number
h	Handling time	s
GLM	Generalized linear model	–
I	Ingestion rate	number s^{-1}
IBM	Individual based model	–
IQR	Interquartile range	–
K	Half saturation constant	–
l	rms distance	m
L	Gross distance	m
M	Mortality rate	day^{-1}
n	Number	number
N	Number of individuals	number
N2	Stage 2 nauplius	–
N6	Stage 6 nauplius	–
NGDR	Net to gross displacement ratio	–
P	Probability	–
P	Production	number $time^{-1}$
q	Digestion rate	number $hour^{-1}$ or $hour^{-1}$
Q	Digestion time	hour

Abbreviation or symbol	Description	Units
r	Prey detection distance	m
R	Domain radius	m
R^2	Coefficient of determination	–
s	Swimming speed	m s^{-1}
Sb	*Semibalanus balanoides*	–
SD	Standard deviation	–
SE	Standard error	–
Sh	Shearwood number	–
SS	Sums of Squares	–
t	Time	s^{-1}
Δt	Time step	s
T	Temperature	°C
x	Horizontal dimension	–
y	Horizontal dimension	–
z	Vertical dimension	–
α	Significance level	–
β	Selectivity intex	–
λ	Persistence length	m
ρ	Spearman correlation coefficient	–
τ	Persistence time	s

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CHAPTER 1

INTRODUCTION

The life cycle of many species of marine benthic invertebrates includes a planktonic larval phase. Propagules are released into the water column as gametes, embryos, or larvae, and return to the benthos after a period of development that range from hours to years, but is usually on the order of weeks to months (*Bradbury and Snelgrove*, 2001). The planktonic stages are typically small, numerous, and difficult to track; therefore, quantifying the sources of variability in the distribution, transport, and survival of propagules has been a major challenge for fisheries oceanographers and marine ecologists (*Govoni*, 2005; *Metaxas and Saunders*, 2009).

It is generally accepted that cumulative mortality of the planktonic stages is very high based on the fact that the number of individuals released in the water column is several orders of magnitude greater than the abundance of adult benthic stages (*Thorson*, 1950; *Morgan*, 1995). Estimates of rates of mortality in the literature are variable ($e.g.$, 2 to 100%; *Rumrill*, 1990), however, rates which have been measured with confidence are rare (but see *Taggart and Leggett*, 1987; *Lamare and Barker*, 1999). This is due to problems separating the effects of advection, diffusion, and mortality on time variation in larval abundance (*Helbig and Pepin*, 1998), and the assumptions associated with "vertical" population models (*Tapia and Pineda*, 2007; see also *Gentleman et al.*, 2012). Predictions of population dynamics are highly sensitive to variability in rates of mortality (*Underwood and Fairweather*, 1989; *Houde*, 2002; *Neuheimer et al.*, 2010); therefore, the difficulty associated with obtaining empirical estimates with accuracy and precision has contributed to the inability to develop robust models that predict population connectivity and recruitment

variability (*Houde*, 2002; *Metaxas and Saunders*, 2009).

In addition to affecting population dynamics, the potentially high rate of mortality experienced during early life in the plankton is suspected to be a strong selection pressure on the evolution of morphology (*Morgan*, 1989), behaviour (*Ohman*, 1988), and life history strategies (*Strathmann*, 1985) of marine benthic invertebrates. Consequently, the relative importance of the various sources of larval mortality is of interest in the fields of both ecology and evolution. Potential sources of mortality of meroplankton include failure in fertilization of gametes, endogenous developmental abnormalities, physiological stress ($e.g.$, sensitivity to temperature, salinity, oxygen, pollution *etc.*), disease, transport away from suitable habitat for settlement, starvation, and predation (*Thorson*, 1950; *Heath*, 1992).

Predation is considered to be a major source of mortality because there is a high diversity of potential predators in the plankton, and larvae are seemingly vulnerable to these predators due to their small size and limited sensory and swimming abilities (*Thorson*, 1950; *Young and Chia*, 1987; *Morgan*, 1995). However, studies which have confirmed natural predators from *in situ* observations of larvae in the digestive tract ($e.g.$, *Lebour*, 1922; *Short et al.*, 2013), and quantified rates of predation ($e.g.$, *Johnson and Shanks*, 2003; *Sorochan and Metaxas*, 2015) are scarce. Much more research on larval predation has been conducted on fish. The fish literature is a valuable tool for insight into the importance of predation on larval marine benthic invertebrates because both taxa have planktonic early stages and similar larval durations (*Bradbury and Snelgrove*, 2001). Comparisons between marine benthic invertebrates and fish are probably most relevant in the earliest stages of development of fishes, when locomotion and sensory abilities are limited.

Rates of predation of planktonic organisms can be characterized as rates of clearance ($i.e.$, search) ingestion, and mortality. The densities of predator and prey and rates of search and ingestion have long been identified as variables that influence rates of mortality due to predation in ecology ($e.g.$, *Holling*, 1959a). The ingestion rate (prey consumed time^{-1} predator^{-1}) is a measure of the rate of prey consumption, and can be converted to a clearance rate (volume time^{-1} predator^{-1}) by dividing by the concentration of prey. The clearance rate is the rate in which a predator processes ($i.e.$, searches) a volume of water for prey (*Båmstedt et al.*, 2000). An instantaneous mortality rate (time^{-1}) can be obtained by multiplying the clearance rate by the concentration of predators (*Kiørboe*, 2008).

Characterization of the components of the process of predation is critical for the development of hypotheses from empirical observations of rates of predation ($e.g.$, *Pepin et al.*, 1992). A conceptual model of the "predation process" is illustrated in Figure 1.1. This model can be made quantitative by developing equations for the rates of search, encounter, and ingestion. Each of these rates is influenced by morphological and behavioural traits of the prey and their predators; therefore, the predation process provides a link between the phenotypes of individuals and the dynamics of populations, which can be evaluated in trait-based models ($e.g.$, *Menden-Deuer and Kiørboe*, 2016).

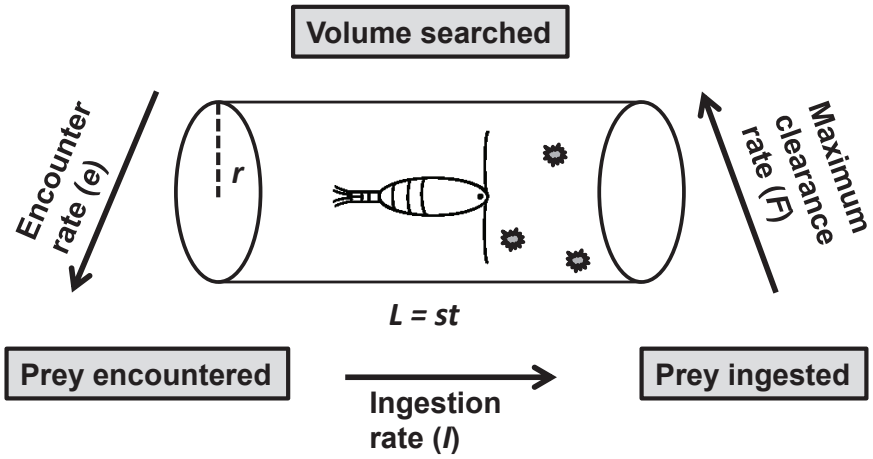

Figure 1.1: Schematic of the search, encounter, and ingestion components of the "predation process". The rates of search (F), encounter (e), and ingestion (I) are depicted by the arrows between boxes. The cylinder represents the volume searched for prey (grey particles) by a predator (copepod) with a prey detection distance, r, travelling along a linear trajectory of length L at speed s over time, t.

In this introduction, I summarize methods for quantitative prediction of rates of ingestion, clearance, and mortality from the predation process. I then outline the methods and results from three different approaches that have been used to derive these rates for larval marine benthic invertebrates and fish from observations of (1) gut content, (2) losses from predation in field-deployed enclosures, and (3) predation *in situ*. I link each approach to components of the predation process, discuss their advantages and limitations with specific reference to problems with scale, and provide recommendations for future research.

Previous reviews on mortality of larval marine benthic invertebrates have been focused on the identification of potential predators from observations *in situ* and *in vitro* (*Young and Chia*, 1987), the ingestion of larvae by predators in the laboratory experiments (*Rumrill*, 1990; *Morgan*, 1995), or larval adaptations that may reduce susceptibility to predators (*Morgan*, 1995; *Vaughn and Allen*, 2010). In this review, I focus on theoretical and empirical methods (and their linkages) that can be used to increase the ability to predict the impact of predators on the mortality of early stages of both marine benthic invertebrates and fish.

1.0.1 Quantifying the predation process

The predation process (Figure 1.1) is governed by the following primary components: search, encounter, and ingestion ($e.g.$, *Bailey and Houde*, 1989). The rate at which a planktonic predator searches its environment is typically expressed as a maximum clearance rate, F, defined as the rate in which a volume of water is searched for prey assuming all prey that are encountered are ingested (*Kiørboe*, 1997). The first equations for the prediction of F were developed more than century ago to characterize the rate of collisions among molecules in a gas (*Maxwell*, 1860) or colloid particles (*Smoluchowski*, 1916). In these models, F is influenced by the distance at which prey are detected by the predator and the relative movements of predator and prey, which are either diffusive ($i.e.$, the magnitude of displacement is proportional to time$^{0.5}$; *Fenchel*, 1984) or ballistic ($i.e.$, the magnitude of displacement is proportional to time; *Gerritsen and Strickler*, 1977). Models for the prediction of F have been developed further to include the effects of swimming direction (*Gerritsen*, 1980), turbulence (*Rothschild and Osborn*, 1988; *Evans*, 1989), and persistence in random direction of travel over the transition from diffusive to ballistic movement (*Visser*, 2007; *Sorochan et al.*, 2017).

The population total encounter rate (encounters volume^{-1} time^{-1}), E is estimated by:

$$E = FC_{prey}C_{pred} \tag{1.1}$$

Where C_{prey} and C_{pred} are the concentration of prey and predators, respectively (*Gerritsen and Strickler*, 1977; *Kiørboe*, 1997). The encounter rate, E, can be converted to (1) a per capita encounter rate (prey encountered time^{-1} predator^{-1}) by dividing by the predator concentration, $e = E/C_{pred} = FC_{prey}$; or (2) a mortality rate by dividing by the

concentration of prey, $M = E/C_{prey} = FC_{pred}$ (***Kiørboe***, 2008). I emphasize that E, e, and M have different dimensions; yet, all have been referred to as "encounter rates" ($e.g.$, *Greene*, 1983; ***Kiørboe***, 2008). The product of the probability of capture after encounter ($i.e.$, susceptibility of prey) and e is referred to as the vulnerability of the prey (*Greene*, 1983). Therefore, the term "vulnerability" is used to describe the ingestion rate (prey ingested time^{-1} predator^{-1}) assuming the predator is not satiated.

Satiation occurs when handling time ($i.e.$, time required to capture, consume, and digest prey) interferes with the ability to ingest prey. A predator cannot feed on prey that are readily available ($i.e.$, highly concentrated) when it is pre-occupied with the process of capture, ingestion, and digestion of other prey. *Holling* (1959b) derived the famous "disk equation" for the prediction of the ingestion rate, I, from C_{prey}, F , and prey handling time, h.

$$I = \frac{FC_{prey}}{1 + FC_{prey}h} \tag{1.2}$$

If F is constant, the relationship between I and C_{prey} is identical to the non-linear (concave downward) curve characterized by the Michaelis-Menten equation (*Gentleman et al.*, 2003; ***Kiørboe***, 2008). The value of F may decrease at low prey concentrations and in the presence of alternative prey, and adjustments to Equation 1.2 have been proposed to account for these situations (*Pepin*, 1987; *Gentleman et al.*, 2003).

Applying Equations 1.1 and 1.2 to spatial scales over which patchiness occurs in nature is problematic because it is assumed that prey are homogenously distributed in space (*Ives et al.*, 1999). Prey patchiness may influence the prey-searching behaviour of the predator, resulting in aggregation of predators within a prey patch ($e.g.$, *Menden-Deuer and Grünbaum*, 2006). Modelling exercises have indicated that patchiness of prey may be disadvantageous to prey if predators aggregate within patches of relatively low prey density, but may be advantageous to prey if the concentration of prey within a patch is high (because predators are swamped), or if predators do not aggregate within a patch of prey (*Nachman*, 2006). Analytical and individual-based models have been developed from prediction of the rate of prey ingestion from prey concentration and prey patchiness (*Ivlev*, 1964; *Vlymen*, 1977; *Nachman*, 2006).

Even though Equations 1.1 and 1.2 are idealized models with restrictive assumptions, their application requires a considerable amount of species-specific data on the movement

of the predator and prey, the distance at which the predator can detect prey, susceptibility of the prey to the predator, and handling time. These variables may be affected by environmental conditions such as light level (*Vinyard and Obrien*, 1976), turbulence (*MacKenzie et al.*, 1994), temperature (*Podolsky and Emlet*, 1993). Advances in the development of mathematical models for the components of the predation process will improve the ability to develop new quantitative hypotheses regarding the mechanisms responsible for variability in the rate of ingestion and mortality of prey.

Observations are required to test the assumptions of these models and quantify the variables required for parameterization of the search, encounter, and ingestion components. Data needed to parameterize components of the predation process on meroplanktonic early life stages of marine benthic invertebrates are scarce (but see *Chia et al.*, 1984; *Lindquist and Hay*, 1996; *Bullard et al.*, 1999), and very few studies have addressed the search, encounter, and ingestion components (but see *Hansson and Kiørboe*, 2006). In contrast, a wealth of these data has been collected for larval fish (*Blaxter*, 1986; *Miller et al.*, 1988; *Fuiman*, 1994; *Kiørboe and MacKenzie*, 1995). This has facilitated the development of hypotheses regarding the importance of the magnitude and variability of size and growth rate of larval fish to their mortality rate due to predation (*Rice et al.*, 1993; *Cowan Jr et al.*, 1996).

In the following section, I review three main approaches used to obtain data on rates of predation on planktonic early life stages of marine benthic invertebrates and fish from empirical observations. In each approach, I indicate how the method is linked to the underlying theory of the predation process.

1.0.2 Approaches for the quantification of rates of predation from empirical observations

1.0.2.1 Quantification of rates of predation from *in situ* observations of gut content

The ingestion rate, I, can be estimated from gut content of predators collected *in situ* using a model that predicts the rate of change of gut content from the rates of ingestion and digestion ($i.e.$, rate of change of gut content = ingestion rate - digestion rate):

$$\frac{\mathrm{d}G}{\mathrm{d}t} = I - qG^b \tag{1.3}$$

Where I is the ingestion rate, q is the rate of digestion, G is the gut content, and b is a constant (*Pennington*, 1981). The parameter b determines the shape of the gastric

evacuation curve that describes depletion of food in the gut over time. For example, if b = 0, the reduction of prey in the gut is linear over time, and if b = 1 the reduction of prey in the gut is exponential over time (*Jobling*, 1981; *Bromley*, 1994). The dimensionality of q is dependent on the value of b; q is expressed as number or mass time^{-1} if the relationship is linear, and time^{-1}, if the relationship is exponential (*Bochdansky and Deibel*, 2001).

Following *Pennington* (1981), Equation 1.3 can be expressed as:

$$I = q\bar{G}^b + \frac{\bar{G}_t - \bar{G}_0}{t} \tag{1.4}$$

Where G_0 and G_t are the initial and final gut contents over t, and the horizontal bars indicate mean values. As t increases, the magnitude of the second term on the right hand side of Equation 1.4 decreases, and the ingestion rate tends toward the digestion rate (*Pennington*, 1981). If it is assumed that $\mathrm{d}G/\mathrm{d}t = 0$ and $b = 1$, Equation 1.4 reduces to the classic model derived by *Bajkov* (1935):

$$I = \frac{\bar{G}}{\bar{Q}} \tag{1.5}$$

where $\bar{Q}$ is the mean "digestion time" ($i.e.$, the time to eliminate a meal from the gut; *Båmstedt et al.*, 2000). Using Equation 1.5, an ingestion rate can be calculated from predator gut content at a single point in time. In turn, a mortality rate, M, can be derived from the ingestion rate and concentration of predators and prey (see Equation 1.1; $M = FC_{pred}$), assuming spatial randomness of predator and prey at the scale of the sampling resolution.

As an alternative to using Equation 1.4, the ingestion rate can be derived from gut content of predators by applying a Poisson distribution to the probability of the number of prey observed within the gut of a predator over a sampling interval. For example, the relationship between the proportion of predators with zero prey in the gut, P(G_0), and the mean number of prey consumed over the sampling interval, $G_{\Delta t}$, is P(G_0) = $-e^{G_{\Delta t}}$ (*Theilacker*, 1995). This approach is most useful for the examination of the impact of predation when the prey of interest represents a minor component of the gut of the predator (*Pepin*, 2006), or from studies in which prey are detected by presence/absence using molecular techniques (*Theilacker*, 1995). Information on the rate of digestion is still required, as it is used to correct for the gut content lost over the period during which the

predator is collected and prey are sampled.

The advantage of studies that derive rates of ingestion, clearance, and mortality of prey from gut content is that they are not reliant on ingestion or clearance rates measured from feeding incubations, which are well known to be influenced by container effects (*de Lafontaine and Leggett*, 1987; *Gibbons and Painting*, 1992). However, uncertainties associated with the effects of predator collection on gut content, the quantification of the digestion time, potential biases associated the assumptions of gut evacuation models (Equations 1.4 and 1.5), and spatial and temporal overlap of predator and prey are of concern (*Hunter and Kimbrell*, 1980; *Jobling*, 1981; *Purcell et al.*, 2014).

The effect of predation on populations of copepods and fish eggs has also been quantified as the ratio of the rates of prey ingestion and prey production ($e.g.$, *Hunter and Kimbrell*, 1980; *Kimmerer*, 1984). Simultaneous estimates of rates of propagule production and consumption by predators do not appear to have been made for marine benthic invertebrates. This metric would provide additional information on the ability of the predator population to suppress larval abundance. Estimates of larval mortality from gut content of predators may be overestimated if larval production is not taken into account because the concentration of prey used to estimate the clearance rate of the predator does include newly produced larvae that have been immediately consumed.

Studies on predation of larval marine benthic invertebrates are scarce and restricted to ctenophore and jellyfish predators and larval barnacle and bivalve prey (Table 1.1). Larval barnacles and bivalves are typically highly concentrated in coastal waters and have a hard covering (exoskeleton or shell) that may reduce the rate of digestion. Both these factors improve opportunistic detection of predation from gut contents, but will likely result in low estimates of prey ingestion, clearance, and mortality, unless the predator is abundant and exhibits strong selectivity for these prey types.

Table 1.1: A summary of studies that have evaluated the potential of predation to influence the abundance of planktonic early life stages of marine benthic invertebrates and fish from *in situ* observations of the gut content of predators. Metrics of predation potential include rates of clearance, F ($m^3\ d^{-1}$), and instantaneous mortality, M (d^{-1} or $\%\ d^{-1}$), as well as the ratio of rates of ingestion to production, $I : P$. The magnitude of each metric in this table represents the maximum value reported. The classification of predation potential as "low", "high", "uncertain", or "not specified", refers to the interpretation of the impact of predation on prey abundance by the authors in each study. The sampling duration of "survey" refers to a single snapshot, usually from a large-scale fish or plankton survey.

Prey	Predator	Study area	Sampling duration, frequency	Metric	Predation potential	Reference
			Larval benthic invertebrates			
Barnacle	Ctenophore	Wadden Sea	Months, daily to biweekly	M	Low $M \approx 2\ \%\ d^{-1}$	*Kuipers et al.* (1990)
	Ctenophore	Northwest Arm, Nova Scotia	Months, weekly	M	Low $M \approx 0.01\ d^{-1}$	*Sorochan and Metaxas* (2015)
	Hydromedusa	Texelstroom and Limfjordern	Months, monthly	M	Low $M \approx 0.004\ d^{-1}$	*Hansson and Kiørboe* (2006)
	Scyphomedusa	Limfjordern	Months, monthly	F, M	High $F \approx 3\ m^3\ d^{-1}$, $M > 0.7\ d^{-1}$	*Hansson et al.* (2005)
Bivalve	Scyphomedusa	Limfjordern	Months, monthly	F	Low $F \approx 0.02\ m^3\ d^{-1}$	*Hansson et al.* (2005)
			Fish (eggs)			
Anchovy	Anchovy	Southern California Bight	Days, hourly; 2 years	IP	Uncertain $IP = 0.17$	*Hunter and Kimbrell* (1980)
	Anchovy	Peruvian Coast	Survey; 1 year	$I : P$	Not specified $I : P = 0.08$	*Santander et al.* (1983)

	Anchovy	South African coast	Survey; 3 years	$I : P$	Not specified $I : P$ = 0.03	*Szeinfeld* (1991)
	Sardine	South African coast	Survey; 3 years	$I : P$	High $I : P$ = 0.28	*Szeinfeld* (1991)
	Anchovy	Bay of Biscay	Survey; 2 years	$I : P$	Low $I : P$ = 0.005	*Bachiller et al.* (2015)
	Mackerel	Bay of Biscay	Survey; 2 years	$I : P$	Low $I : P$ = 0.02	*Bachiller et al.* (2015)
	Sardine	Bay of Biscay	Survey; 2 years	$I : P$	High $I : P$ = 0.20	*Bachiller et al.* (2015)
	Scyphomedusae and ctenophores	Chesapeake Bay	Days, hourly	M	High M= 50 % d^{-1}	*Purcell et al.* (1994)
Plaice	Herring	North Sea	Survey; 3 years	$I : P$	Low $I : P$ = 0.02	*Daan et al.* (1985)
Cod	Herring	North Sea	Survey; 3 years	$I : P$	Low $I : P$ = 0.002	*Daan et al.* (1985)
	Herring	Bornholm Basin, Baltic Sea	Survey; 15 years	I and P	High $I : P$ not reported	*Neumann et al.* (2016)
	Sprat	Bornholm Basin, Baltic Sea	Survey; 15 years	I and P	High $I > P$ in some instances	*Neumann et al.* (2016)
	Capelin	Trinity Bay, Newfoundland	Days, hourly	F	Uncertain, F = 0.84 m^3 h^{-1}	*Pepin* (2006)

			Fish (larvae)			
Anchovy	Scyphomedusae	Chesapeake Bay	Days, hourly	M	High M= 55 % d^{-1}	*Purcell et al.* (1994)
	Euphaussids	Coast of Southern California	Days, hourly	M	Not specified M = 0.28 d^{-1}	*Theilacker* (1995)
Walleye Pollock (eggs and larvae)	Crustaceans	Gulf of Alaska	Survey; 2 years	M	High M = 1.2 % d^{-1}	*Bailey et al.* (1993)
Herring	Hydromedusa	Kulleet Bay Vancouver Island	Days, daily	M	High M = 97 % d^{-1}	*Purcell and Grover* (1990)
Fish	Siphonophore	Gulf of California	Months, monthly	M	High M = 28 % d^{-1}	*Purcell* (1981)
	Siphonophore	Gulf of Mexico	Weeks, daily	M	High M = 60 % d^{-1}	*Purcell* (1984)
	Scyphomedusae	Catalan Sea	Survey; 2 years	M	High M = 13% d^{-1}	*Purcell et al.* (2014)

1.0.2.2 Mortality rates estimated from incubations in enclosures

Because meroplankton are difficult to track in the sea, feeding incubations in containers with small volumes ($i.e.$, 10's of litres or less) in the laboratory or enclosures with larger volumes (100's to 1000's litres) deployed in the field have been used to estimate mortality rates from the number of larvae consumed over the incubation period (*Paradis et al.*, 1996). In these experiments, the instantaneous mortality rate is calculated from the number of prey lost to ingestion by the predator over time:

$$M = \frac{\ln(N_t/N_0)}{-t} \tag{1.6}$$

Where, N_0 and N_t are the initial and final number of prey and t is the duration of the feeding incubation. In comparison to large enclosures, small containers allow for more replication and are easier to set up and sample, but their application to nature is constrained by prey densities that are higher than observed in the sea, as well as by container effects caused by interactions between organisms and container walls, and among organisms confined to small volumes.

Large enclosures allow for observations of predation at low prey densities, and reduced container effects. However, interactions between organisms and the walls of containers still occur (*Martin*, 2001), and the volume of the enclosure may need to be large ($i.e.$, 1000's of litres) to ensure that the volume does not affect mortality rates (*de Lafontaine and Leggett*, 1987). Mortality rates on larval fish have been found to decline logarithmically with increasing container volume, which has been attributed to increased heterogeneity in the vertical distribution of prey (*de Lafontaine and Leggett*, 1987). A decline in mortality rates with increasing container size is also assumed to occur with larval marine benthic invertebrates as prey (*Rumrill*, 1990; *Metaxas and Saunders*, 2009; *Vaughn and Allen*, 2010). However, the opposite effect may actually occur if organisms aggregate close to container walls (*Bergström and Englund*, 2004), or if the ability of the predator to feed is negatively affected by the container walls (*Gibbons and Painting*, 1992).

Johnson and Shanks (2003) evaluated predation on larval echinoderms, gastropods, and bivalves, which were seeded into 123-l field-deployed enclosures that contained natural assemblages of zooplankton, as well as seeded predators. Although many potential predators were identified in the enclosures, mortality rates were usually low and no predation often occurred over 24 h at near-natural prey concentrations of ≈ 1 larvae l^{-1}

(Table 1.2). The authors found that ingestion rates of seeded predators increased with prey concentration, and decreased in the presence of other potential prey items ($i.e.$, "background plankton"). This study supports the hypothesis that predation may not always be a major contributor to larval mortality in the sea. With the exception of this study, rates of ingestion on larval marine benthic invertebrates have been restricted to small containers in the laboratory (see reviews by *Rumrill*, 1990; *Vaughn and Allen*, 2010).

Field-deployed enclosures, much larger than those used by *Johnson and Shanks* (2003), have been used far more frequently to study predation on larval fish by adult fish, cnidarian medusa, and ctenophores (Table 1.2). These studies have found that mortality rates increased linearly with the concentration of predators (*de Lafontaine and Leggett*, 1988) and were independent of the concentration of prey (*de Lafontaine and Leggett*, 1987, 1988; *Gamble and Hay*, 1989; *Fuiman and Gamble*, 1989; *Cowan et al.*, 1992). These results are consistent with the dynamics predicted by encounter rates (Equation 1.1). That is, the clearance rate was not affected by the presence of other predators, the predators did not cease feeding at low prey concentrations, and the predators were not satiated at high prey concentrations. Studies that evaluated the effect of predation in the presence of other zooplankton (in addition to prey items of interest) have found that that mortality rates were either reduced (*Cowan and Houde*, 1993) or did not change (*de Lafontaine and Leggett*, 1987; *Cowan et al.*, 1992).

In a meta-analysis of studies from Table 1.2 (and data from other sources), *Paradis et al.* (1996) found that mortality rates decreased as the ratio of prey to predator size increased with respect to predation by cnidarian medusa, and that the relationship between the same variables was dome shaped with respect to predation by larval fish and ctenophores. These results are consistent with conceptual models developed *Bailey and Houde* (1989) based on opposing effects of prey size on the encounter rate and prey susceptibility. *Bailey and Houde* (1989) predicted (1) the encounter rate increases with the size of prey due to increases in the swimming speed and ability of the predator to detect prey, and (2) the susceptibility of prey decreases with the size of the prey due to an increased ability of prey to escape attack.

Table 1.2: A summary of studies that have evaluated the potential of predation to influence the abundance of planktonic early life stages of marine benthic invertebrates and fish using enclosures deployed in the sea. The classification of predation potential as "low", "high", or "not specified"(NA) refers to the interpretation of the impact of predation on prey abundance by the authors in each study. We report the maximum observed mortality rates, M, in each study, unless stated otherwise. Values of, M, provided by Johnson and Shanks (2003) for larval benthic marine invertebrates are not standardized by predator abundance (units d^{-1}), whereas mortality rates for larval fish, M_p are standardized ($i.e.$, units predator^{-1} d^{-1}).

Prey	Predator	Volume (l)	Time (h)	Predation potential (d^{-1})	Reference
			Larval benthic invertebrates		
Bivalve	Dinoflagellate	123	24	High; M = 0.07	*Johnson and Shanks* (2003)
	Stickleback			Low; M = 0.003	
	Hydromedusa			Low; M = 0.005	
	Larval polychaete			Low; M = 0.003	
			Larval fish		
Capelin	Hydromedusa	3200	36 to 96	High; M_p = 0.14	*de Lafontaine and Leggett* (1988)
	Hydromedusa			High; M_p = 0.45	
	Scyphomedusa			High; M_p = 0.23	
	Scyphomedusa			High; M_p = 1.59	
	Scyphomedusa	3207	36 to 45	NA; M_p = 0.17	*de Lafontaine and Leggett* (1987)
	Scyphomedusa	3100	6	NA; M_p = 0.10	*Elliott and Leggett* (1996)
	Stickleback			NA; M_p = 0.09	
	Hydromedusa	3200	40	High; M_p = 0.07 (mean)	*Litvak and Leggett* (1992)
	Stickleback			High; M_p = 0.89 (mean)	
	Stickleback	2700	24	High; $M_p \approx 5$	*Pepin et al.* (1992)
Herring	Scyphomedusa	5000	24-27	Low; M_p = 0.018	*Gamble and Hay* (1989)
	Herring	15800	2 to 8	NA; $M_p \approx 0.50$	*Fuiman and Gamble* (1989)
	Herring	15800	24	Low; M_p = 0.06	*Fuiman and Gamble* (1988)

	Sprat			High; M_p = 3.25	
	Sandeel			High; M_p = 1.56	
	Sandeel			High; M_p = 0.60	
Black drum and anchovy (eggs)	Hydromedusa	2200	24	High; M_p = 0.09	*Cowan et al.* (1992)
	Ctenophore			High; M_p = 0.05	
Goby (eggs and larvae)	Scyphomedusa	3200	24	NA; M_p = 0.57	*Cowan and Houde* (1993)
	Ctenophore			NA; M_p = 0.06	
	Anchovy			NA; M_p = 0.67	

1.0.2.3 Observation of predation *in situ*

Hansson (2006) presented an approach in which the predator is (1) held in the laboratory until its gut contents are fully digested, (2) tracked by divers in the sea over a given feeding period, and (3) collected for analysis of gut contents. Over the feeding period, plankton is sampled in close proximity to the predator, which allows for the calculation of an *in situ* clearance rate, which can then be extrapolated to a mortality rate for a given concentration of predators (see Equation 1.1). *Hansson* (2006) developed this method for evaluation of predation by large cnidarian medusae that move relatively slowly in the water column and may feed at a high rate over a relatively short period.

Perhaps the most convincing study that documented the detrimental effect of predation on meroplankton has involved direct observations by divers of predation on ascidian tadpole larvae by planktivorous fish on the Great Barrier Reef (*Olson and McPherson*, 1987). This is the only study that has quantified losses of larvae by direct observation of the larvae, partly because the method requires that the larvae are large enough to follow under water, and possess a very short pelagic larval duration ($i.e.$, hours). Predation has also been measured from losses of larvae that have been teathered to a surface over a specified sampling interval (*Acosta and Butler*, 1999; *Allen and McAlister*, 2007). These methods are obviously unrealistic because larval movement is restricted. Larval teathering has been used to test hypotheses on relative predation in different habitats (*Acosta and Butler*, 1999; *Allen and McAlister*, 2007). Instantaneous mortality rates can be derived from the proportion of larvae that survived and the time over which larvae were followed (or teathered) using Equation 1.6.

1.0.3 Recommendations for future research

To avoid bias, studies must be conducted at scales relevant to the question at hand (*Taggart and Frank*, 1995). Processes (including predation) critical to survival and distribution of meroplankton operate over a range of overlapping scales, and this presents a problem for research on recruitment and population connectivity (*Govoni*, 2005; *Metaxas and Saunders*, 2009). For predation, the relevant scales of interest are those in which overlap ($i.e.$, encounters) occur between predators and prey. In the horizontal dimension, these scales are on the order of weeks to months, and kilometers, whereas in the vertical dimension they are on the order of minutes to days and centimeters to meters, respectively (*Govoni*, 2005). Characterizing the variability in overlap of predators and prey in time

and space is critical (*Paradis et al.*, 1996; *Purcell et al.*, 2014), and a major challenge associated with obtaining accurate estimates of mortality due to predation. In this review, I have summarized theoretical and empirical methods for the evaluation of rates of mortality due to predation on the planktonic early life stages of marine benthic invertebrates and fish (Table 1.3). Not surprisingly, all these methods have problems associated with scale.

Table 1.3: Data requirements, assumptions, advantages, and limitations of methods that use empirical observations to quantify rates of mortality of marine benthic invertebrate larvae from rates of ingestion.

Method	**Data**	**Assumptions**	**Advantages**	**Limitations**
Gut content	G b q C_{prey} C_{pred}	b accurately describes gastric evacuation curve Homogenous distribution of C_{prey} and C_{pred} over time	Data collected *in situ* Data can be collected over larval duration of prey	Assumptions are difficult to validate Intensive sampling
Enclosure	N_0 N_t	Constant M over time, t	Natural C_{prey} and C_{pred} Replication Results comparable across studies Hypothesis testing	Container effects Data applicable to short time scale (days) only
Direct observation (of prey)	N_0 N_t	Constant M over time, t No effect of diver (observer)	Prey tracked *in situ*	Data applicable to short time scale (hours) only

The derivation of a mortality rate from an ingestion rate ($i.e.$, manipulation of Equation 1.1) requires the assumption that predation occurs within an environment characterized by a uniform concentration of predators and prey. Concurrent data of the vertical distribution and migratory patterns of the predator and prey are therefore required to ensure

that (1) the gut content reflects feeding that occurred at the concentration of prey that was sampled, and (2) the concentration of predators and prey reflects overlapping densities (*Purcell et al.*, 2014).

When ingestion is predicted from gut contents, the clearance rate is often calculated from a single sampling event and extrapolated to a daily rate, which is then used to project losses over the entire larval duration ($e.g.$, *Hansson et al.*, 2005). Predator-prey overlap can vary on time scales associated with tidal or diel cycles due to vertical migratory behaviour of zooplankton (*Forward and Tankersley*, 2001; *Cohen and Forward*, 2009), and is often not captured at relevant scales of $<$ 1 day ($e.g.$, *Sorochan and Metaxas*, 2015). Ideally, sampling should be conducted on the scale of hours over a 24-h period, and at several times over the larval duration. To avoid biases in gut content associated with collection of predators from plankton nets, predators are usually collected individually from the surface or by divers (*Purcell et al.*, 2014). Therefore, hourly sampling may not be possible in darkness, or if the time required to sample a single batch of predators is several hours.

It is very difficult to validate the assumptions associated with the estimation of rates of ingestion, clearance, and mortality of meroplankton from the gut contents of predators and the abundance of predator and prey in the field. Therefore, I recommend this method be used to identify predators that may be of potential importance in reducing the numbers of larval populations, rather than for obtaining accurate measurements of ingestion, clearance, or mortality rates, *per se*. A complete representation of the impact of predation would also require that samples be collected at different locations ($e.g.$, adjacent inlets or bays). Clearly, this type of study requires intensive sampling, particularly if the prey item rarely occurs in the gut of the predator ($e.g.$, *Pepin*, 2006).

Measurements of rates of mortality in large enclosures allow for the establishment of vertical heterogeneity of the prey field. However, the size of the enclosure can influence the distribution of organisms, and consequently, the loss of prey over the experimental duration (*de Lafontaine and Leggett*, 1987). Enclosure walls certainly impact hydrodynamic conditions that could otherwise influence vertical distribution of prey. Results from these studies are limited to the time scale of the feeding incubation (usually $<$ 48 h), and the sizes and developmental stages of the predator and prey tested, and should therefore not be extrapolated to mortality experienced over the entire larval duration.

Direct observations of predation in which the predator or prey are followed by divers are

restricted to the short durations in which divers can be underwater. Therefore, observations of prey consumption are restricted to very specific environmental conditions, and rates of mortality at very short larval durations. Although these studies appear to be logistically difficult to conduct, parallel studies to that done by *Olson and McPherson* (1987) would be valuable in determining the repeatability of their observations and how predation may vary in other habitats and geographical regions.

Despite the limitations associated with each method, and low number of observations that have been made, studies on predation of larval marine benthic invertebrates indicate that individuals are not always subjected to intense predation over their pelagic duration (*Johnson and Shanks*, 2003; *Sorochan and Metaxas*, 2015). Instead, predation may be important in regulating the abundance of larvae in certain instances, as there are examples of substantial consumption of larval benthic invertebrates from each of the methods that I reviewed (*Olson and McPherson*, 1987; *Johnson and Shanks*, 2003; *Hansson et al.*, 2005). Results from studies of ingestion rates derived from gut content and losses in enclosures generally support the notion that predation is (at times) a potentially important source of mortality of larval fish (Tables 1.1 and 1.2). Many of these studies were conducted on eggs or early larval stages; therefore, these results are probably also relevant to larval marine benthic invertebrates of comparable size.

It is generally accepted that mortality is highly variable in space and time (*Vaughn and Allen*, 2010). The development of a unifying theory on factors that influence the survival of pre-recruits in the sea may not be possible due to variability among taxa and life history strategies, and variability in environmental conditions within ecosystems (*Day and McEdward*, 1984; *Bailey and Houde*, 1989; *Govoni*, 2005). This does not preclude the quantification of rates of predation (and other sources of mortality) on planktonic early life stages. Meroplankton may be subjected to a "gauntlet" of different predators over the larval duration, and the potentially important predators need to be identified by the quantification of ingestion, clearance, and mortality rates. As pointed out by *Bailey and Houde* (1989), this is probably most easily done in relatively simple ecosystems with low taxomonic diversity and predictable seasonal cycles that occur at high latitudes.

Each approach that I have reviewed has different advantages and limitations (Table 1.3); therefore, I encourage future research using each method, and highlight the importance of theoretical and experimental studies that aim to improve and parameterize mathematical

models in the predation process (Figure 1.1). I emphasize that the problem of scale should be carefully considered when designing experiments and interpreting results. Quantification of the predator and prey overlap at scales of meters and hours represents a major challenge using conventional sampling techniques. Spatial and temporal variability in overlap can be potentially simulated from particle tracking in ocean models; however, this requires extensive data on the vertical distribution and migratory behaviour of both predator and prey, and there are potential problems associated with the number of particles that may be required (*Miller*, 2007).

1.0.4 Thesis Objectives

The overall objective of this thesis is to improve the ability to predict the ecological significance of predation in the mortality of planktonic larval stages of marine benthic invertebrates. I have conducted: (1) a modeling study to provide methods for prediction of the rate of search of a planktonic predator for prey based on the motility characteristics of prey; (2) laboratory experiments to quantify larval motility characteristics, their variability with environmental conditions, and their applicability to the model developed in (1); and (3) field observations to examine the potential impact of a known planktonic predator on larval stages of a marine benthic invertebrate. Components (1) and (2) can be combined to develop quantitative hypotheses regarding the effects of the behaviour of individuals observed at small scales ($i.e.$, centimeters and minutes) on rates of mortality due predation at the population level, whereas component (3) uses field and laboratory observations in combination with theoretical concepts of search, encounter, and ingestion (Figure 1.1) to obtain estimates of potential predation impact (as described in this chapter).

This thesis is arranged into 5 chapters including this Introduction. **Chapters 2 to 4** are intended as standalone manuscripts for publication in the primary literature; therefore, there is repetition in some content among the chapters. **Chapters 2 and 4** have been published (*Sorochan and Metaxas*, 2015; *Sorochan et al.*, 2017), and **Chapters 3** has been accepted for publication. In **Chapter 2**, I develop an individual-based model to simulate the effects of directional persistence ($i.e.$, the tendency of a random walker to maintain direction of travel) on the rate of search for prey of an ambush-feeding predator. I used the model to evaluate predictions of the rate of search from unsubstantiated formulae in the literature, and to describe the variability in the rate of search over a range of scales of directional persistence and prey detection distance that are relevant to predation on

mesozooplankton (including larval marine benthic invertebrates). In **Chapter 3**, I (1) quantify directional persistence in the movement (swimming and sinking) of different larval stages of barnacles over a range temperatures that these larvae may experience in the sea, and (2) test the null hypothesis of isotropy in larval motility, which is a movement assumption in the model developed in **Chapter 2**. In **Chapter 4**, I estimate the potential predation impact (expressed as an instantaneous mortality rate) of a species of ctenophore on the abundance of larval barnacles. I derive the mortality rate from observations of the number of larval barnacles in the pharynx of ctenophores collected from the field, the density of ctenophores and larval barnacles in the field, and the time required to for ctenophores to digest larval barnacles in the laboratory.

In this thesis, I demonstrate how theoretical and empirical approaches, which have been established in plankton feeding ecology, can be applied to questions regarding the ecology of larval marine benthic invertebrates. I show how mechanistic modelling and observations made *in vitro* can be combined to develop quantitative hypotheses, and conduct a field study to evaluate the importance of predation on planktonic propagules of marine benthic invertebrates by a planktonic predator. Overall, this thesis will contribute to the ability of larval ecologists to develop hypotheses regarding the effect of predation on the evolution and dynamics of the planktonic propagules of marine benthic invertebrates.

CHAPTER 2

MODELLING RATES OF RANDOM SEARCH OVER THE TRANSITION FROM DIFFUSIVE TO BALLISTIC MOVEMENT OF PLANKTON

2.1 Abstract

The rate of search for food ($i.e.$, maximum clearance rate), F, of a plankter is essential to the prediction of encounter rates, and is dependent on movement. Classic encounter rate models assume diffusive or ballistic movements, which represent opposing extremes of directional persistence. From the perspective of the predator, the directional persistence of prey is determined by the ratio of the persistence length ($i.e.$, "run length" of a random walker), λ, and the radius of prey detection, r. I developed an individual-based model to (1) describe variation in F due to λ/r and time, and (2) evaluate the utility of published corrections (that take into account the effect of λ/r on F) to the classic models. My results illustrate that classic models overestimate F when their assumptions of movement are

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My coauthors Dr. Wendy Gentleman and Dr. Anna Metaxas supervised the study design and analysis, and edited the manuscript.

invalid, and indicate that the effect of time-variation in F on food consumption is most substantial near the middle of the diffusive to ballistic transition ($i.e.$, $\lambda/r \approx 1$). At $\lambda/r << 1$, predators may exploit high clearance rates by "jumping", provided that the far-field concentration of prey is sufficiently high. I recommend a published Michaelis-Menten type correction to the classic models, and discuss the assumptions and applications of the model system.

2.2 Introduction

Encounters are the initial step in ecological processes that affect growth, mortality, and reproduction of planktonic organisms. These processes include nutrient absorption (*Pasciak and Gavis*, 1974), feeding (*Kiørboe et al.*, 1985), mating (*Kiørboe and Bagøien*, 2005), and fertilization of propagules released by broadcast spawners (*Pennington*, 1985). Encounter rate models are therefore important tools for the development of mechanistic models that predict plankton dynamics (*Gerritsen and Strickler*, 1977; *Kiørboe*, 2011; *Litchman et al.*, 2013).

The encounter rate, E, among individuals from two populations is modelled as the rate of a chemical reaction. That is, the product of the concentration of reactants, A and B, and a rate constant, F ($i.e.$, E = F[A][B]; *Gardiner*, 1969). In plankton feeding ecology, the "reactants" are the predator and prey, and the "rate constant" is the maximum clearance rate (dimensions of volume time^{-1}), defined as the rate in which the predator searches for prey assuming all encountered prey are ingested ($e.g.$, *Kiørboe*, 1997). In *Holling* (1959b)'s famous disk equation for the type II functional response, the maximum clearance rate is referred to as the "rate of discovery" (also known as the "attack rate"). The maximum clearance rate is dependent on the distance in which prey can be detected from the predator and the movement of both the predator and the prey. Movement affects the maximum clearance rate because backtracking decreases the rate in which previously unexplored water is searched ($e.g.$, *Levandowsky et al.*, 1988).

Classic analytical models for prediction of the maximum clearance rate were originally derived to predict the rate of collisions among spherical particles moving in random directions (*Maxwell*, 1860; *Smoluchowski*, 1916). These models have been adopted or re-discovered in plankton ecology to predict encounter rates caused by movement of the predator and prey that is diffusive ($i.e.$, due to diffusion; *Pasciak and Gavis*, 1974; *Fenchel*,

1984) or ballistic ($i.e.$, linear; *Gerritsen and Strickler*, 1977; *Hutchinson and Waser*, 2007). Both models have been strongly influential in the development of mechanistic theory in zooplankton feeding ecology ($e.g.$, *Kiørboe*, 2011).

Diffusive and ballistic movement are extremes on a continuum of directional persistence, defined as the tendency of an individual to maintain its direction of travel over time (*Codling et al.*, 2008). In a movement model known as correlated random walk (CRW), directional persistence is parameterized as "persistence time", defined as the time before reorientation in a random direction in discrete ($i.e.$, "run and tumble") movement (*Visser and Thygesen*, 2003). The corresponding "persistence length" is the product of the persistence time and particle speed (*Fuchs*, 1964). Diffusive or ballistic movement apply when directional persistence is perceived as negligible or substantial, respectively, from a particular time or length scale. From the perspective of a predator with a spherical perceptive field, the directional persistence of prey is dependent on the ratio of the persistence length of prey to the radius of prey detection of the predator (*Visser and Kiørboe*, 2006). For example, when the persistence length is much smaller or larger than the radius of prey detection, movement is perceived as diffusive or ballistic, respectively.

Classic models can give erroneous predictions of the maximum clearance rate of a planktonic predator if the assumptions of diffusive or ballistic movement are not valid (*Visser and Kiørboe*, 2006). The limitations of the assumptions of either diffusive or ballistic movement on prediction of the maximum clearance rate have been acknowledged in the physical sciences for decades. However, derivation of an analytical model for the maximum clearance rate over the transition from diffusive to ballistic movement is difficult, and has therefore been limited to approximations that are "rough estimates" ($e.g.$, *Fuchs*, 1964) or only applicable to part of the diffusive to ballistic transition ($e.g.$, *Harris*, 1982). Correlated random walk bridges the gap between diffusive and ballistic movement; however, linking directional persistence and particle encounter remains a challenge in the field of encounter theory.

This study aims to: (1) improve the ability to predict the maximum clearance rate over the diffusive to ballistic transition in movement; and (2) describe the variability in the maximum clearance rate due to diffusive, ballistic, and CRW movement over scales of prey detection and directional persistence of movement relevant to zooplankton feeding. I present an individual-based model (IBM) as a reliable tool for prediction of the maximum

clearance rate from CRW movement, and evaluate the utility of previously published analytical models ($e.g.$, *Fuchs*, 1964; *Harris*, 1982; *Visser*, 2007).

2.3 Methods

I developed an individual-based model (IBM) to predict maximum clearance rate, F_{IBM}, of a non-moving predator that can detect prey within a spherical field characterized by radius, r. Encounters between the predator and prey were facilitated by correlated random walk (CRW) movement of the prey (*Taylor*, 1922; *Dunn*, 1983; *Codling et al.*, 2008). This model system is therefore directly applicable to ambush feeding predators ($e.g.$, chaetognaths or copepods of the genus *Oithona*) that do not actively search for prey, but attack prey upon encounter or collect prey that collide with their surface (*Kiørboe*, 2011).

I qualitatively compared data that emerged from the IBM to solutions from two classic models that assume movement of prey is always diffusive or always ballistic, which I refer to as the "diffusive model" and "ballistic model", respectively. Following (*Smoluchowski*, 1916), the maximum clearance rate predicted from the diffusive model, F_{Diff}, is:

$$F_{Diff} = 4\pi Dr(1 + \frac{r}{(\pi Dt)^{0.5}}) \tag{2.1}$$

where, D is the diffusivity of the prey, and t is time. The diffusivity of a correlated random walker in three dimensions is:

$$D = \frac{s^2\tau}{3} \tag{2.2}$$

where, s is the swimming speed, and τ is the persistence time (*Lovely and Dahlquist*, 1975). It is assumed that all prey are immediately ingested when they are within radial distance r of the predator. Therefore, C_{prey} becomes depleted in a boundary layer surrounding the predator over time. At steady state $F_{Diff} = 4\pi Dr$ (*Koch*, 1971; *Berg*, 1993). Following *Maxwell* (1860), the maximum clearance rate predicted from the ballistic model, F_{Ball}, is:

$$F_{Ball} = \pi r^2 s \tag{2.3}$$

This model is identical to that derived by *Gerritsen and Strickler* (1977) when the predator is motionless.

I also compared data from the IBM to three published corrections to the (steady state) diffusive and ballistic models (see Table A.1 for equations). When multiplied by F_{Diff} or F_{Ball}, the corrections predict values of the realized maximum clearance rate, F, over the diffusive to ballistic transition. The corrections are expressed as F/F_{Diff} or F/F_{Ball}, are bound by 0 and 1, and are dependent on the persistence length of prey movement, λ, and r (*Fuchs*, 1964; *Harris*, 1982; *Visser*, 2007).

2.3.1 Individual based model

I positioned a motionless predator with a perceptive radius, r, at the origin of a spherical domain with radius, R. I selected the initial positions of prey randomly from a uniform distribution excluding positions within a distance r of the origin. I developed a 3D version of *Taylor* (1922)'s 1D CRW to simulate prey movement (Figure 2.1). Prey travelled at a constant speed, s = 1 mm s^{-1}, along linear path segments of equal length over each time step, Δt. At each Δt, individual prey maintained their direction of travel based on a constant probability. Therefore, the probability of maintaining direction, P, decreased exponentially over time, t, at a constant rate, $1/\tau$, where τ is the persistence time of prey movement ($i.e.$, P $= e^{-t/\tau}$), and the corresponding persistence length is $\lambda = s\tau$. I changed the direction of travel of the prey by randomly selecting a displacement in each dimension (x, y, z) from a uniform distribution under the condition that $s\Delta t = (\Delta x^2 + \Delta y^2 + \Delta z^2)^{0.5}$.

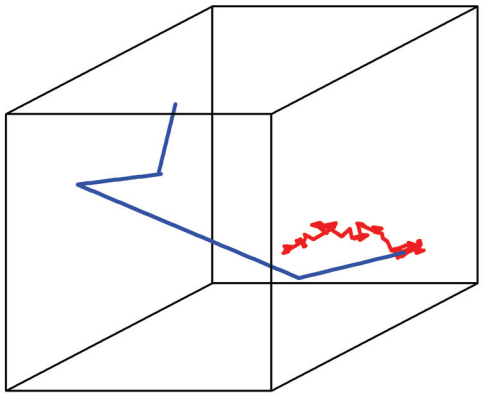

Figure 2.1: Correlated random walks of two particles travelling at the same speed over the same time period. The persistence time, τ, of the particle represented by the blue path was 20 times greater than that of the particle represented by the red path.

At each Δt, I defined an encounter as an event in which the distance between the location of an individual prey item and the predators centre ($i.e.$, the origin) was $\leq r$ (see

Figure A.1 for illustration of encounter criteria). I enumerated the encounters and derived a maximum clearance rate, F_{IBM}, from:

$$F_{IBM} = \frac{e}{C_{prey}} \tag{2.4}$$

where e is the encounter rate (encounters per Δt) and C_{prey} is the initial concentration of prey. I removed prey that were encountered by the predator without replacement; therefore, all encountered prey were "ingested". I selected an appropriate duration of the simulation and value of R such that C_{prey} near the outer boundary did not become depleted. This was confirmed by plotting the relationship between the concentration of prey and the radial distance from r (Figure 2.2). I re-positioned prey that exited the outer boundary of the domain such that their displacement continued through the opposite side, thereby maintaining a no-net-flux boundary condition.

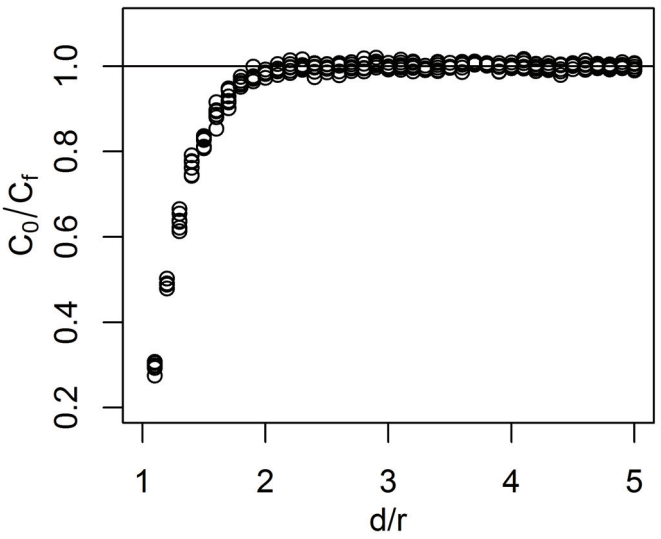

Figure 2.2: The relationship between the ratio of the initial to final prey concentration, C_0/C_f, and the ratio of radial distance from the origin to the radius of prey detection, d/r. Data from 6 replicate simulations are shown in which the persistence length, λ = 0.1 mm and encounter radius, r = 1 mm.

2.3.2 Simulations

I carried out two different sets of simulations using the IBM. In both simulations, I derived F_{IBM} over a range of values of λ and r that were consistent with zooplankton feeding on

different prey types (Table 2.1). I varied r and R together to maintain a constant ratio of predator to domain volume (Table 2.2).

In the first set of simulations, I ran the IBM for 3 s at a high prey concentration (2.5 x 10^3 prey mm^{-3}) to describe the effect of λ/r on the time variation of F_{IBM} , which is particularly strong when $\lambda << r$. I calculated mean F_{IBM} at each Δt from n = 6 replicate time series of F_{IBM} for each combination of λ and r (Table 2.2). I illustrated the variation in $F_{IBM}(\lambda, r)$ by creating a 2D surface from a bivariate interpolation. Separate surfaces were created for each t.

In the second set of simulations, I ran the IBM for 3600 s at a lower prey concentration (0.1 prey mm^{-3}) to describe time-averaged values of F_{IBM}. I calculated the mean F_{IBM} across the entire time series and then calculated an overall mean across all replicates (n = 5) for each combination of λ and r. I qualitatively compared these results to steady state predictions from formulae (Table A.1) proposed by *Fuchs* (1964), *Harris* (1982), *Visser* (2007). All simulations were run using MATLAB v 2016b; the code for simulations is provided in subsection A.2.2 in Appendix A. Data analysis was done with R v 3.2.2.

Table 2.1: Ranges (presented as order of magnitude) of swimming speed (s), lengths of directional persistence (λ), and reaction distance (r) measured for flagellates, ciliates, copepods and chaetognaths. References: 1, *Visser and Kiørboe* (2006); 2, *Kiørboe* (2011); 3, *Schuech and Menden-Deuer* (2014); 4, *Saiz and Kiørboe* (1995); 5, *Svensen and Kiørboe* (2000); 6, *Kiørboe and Bagøien* (2005); 7, *Bianco et al.* (2014); 8, *Feigenbaum and Reeve* (1977); 9, *Saito and Kiørboe* (2001); 10, *Tönnesson and Tiselius* (2005); 11, *Kiørboe and MacKenzie* (1995) and references therein.

Organism	s **(mm s^{-1})**	λ **(mm)**	r **(mm)**	**Reference**
Ciliates and flagellates	0.01 to 1	0.1 to 1	0.001 to 0.01	1 to 3
Copepods	1 to 10	1 to 10	0.1 to 1	1, 2, 4 to 7
Chaetognaths	0	–	1 to 10	8 to 10
Larval fish	1 to 100	NA	1 to 10	11

Table 2.2: Parameterizations in the individual-based model used to predict the maximum clearance rate, F_{IBM}, in short (3 s) and long (3600 s) simulations.

Parameter	Short	Long
C_{prey} (prey mm^{-3})	2.5 x 10^3	0.1
s (mm s^{-1})	1	1
r (mm)	0.5 to 2 by 0.1	0.5 to 2 by 0.1
R (mm)	$5r$	$100r$
λ (mm)	0.1 to 2 by 0.1	0.5 to 2 by 0.5
Δt (s)	0.1	0.5
t (s)	3	3600
Replicate simulations	6	5

2.4 Results

2.4.1 Time varying clearance rate

Simulations of the time varying clearance rate show that both the diffusive and ballistic models can overestimate the realized maximum clearance rate if used incorrectly, and that the upper limit of the realized maximum clearance rate is F_{Ball}. Even when movement is diffusive, the diffusive model overestimated F_{IBM} at short time scales because F_{Diff} is proportional to $t^{-0.5}$ (Equation 2.1), resulting in F_{Diff} approaching infinity as t approaches zero (Figure 2.3).

For a given r, the effect of time on F_{IBM} increased non-linearly as λ decreased. For example, after 3 s, the difference in F_{IBM}/F_{Ball} between λ/r = 0.05 and λ/r = 0.5 was larger than between λ/r = 0.5 and λ/r = 1 by a factor of $\approx$ 4 (Figure 2.4). The same effect can be visualized in Figure 2.5, wherein the contours of F_{IBM} at 3 s only remain similar to F_{Ball} when λ is large relative to r. In contrast to the simulations run at high prey concentration ($i.e.$, 2.5 x 10^3 individuals mm^{-3}; Figure 2.3), the time series of F_{IBM} at low prey concentration ($i.e.$, 0.1 individuals mm^{-3}) were characterized by episodic spikes that often corresponded to single encounter events (Figure A.2).

2.4.2 Corrections to maximum clearance rate at steady state

Corrections to the diffusive model by *Fuchs* (1964), *Harris* (1982), and *Visser* (2007) generally exhibited similarly shaped relationships with λ/r (Figure 2.6). Conversion from diffusive to ballistic correction using the conversion factor, $F_{Diff}/F_{Ball} = 4\lambda/3r$,

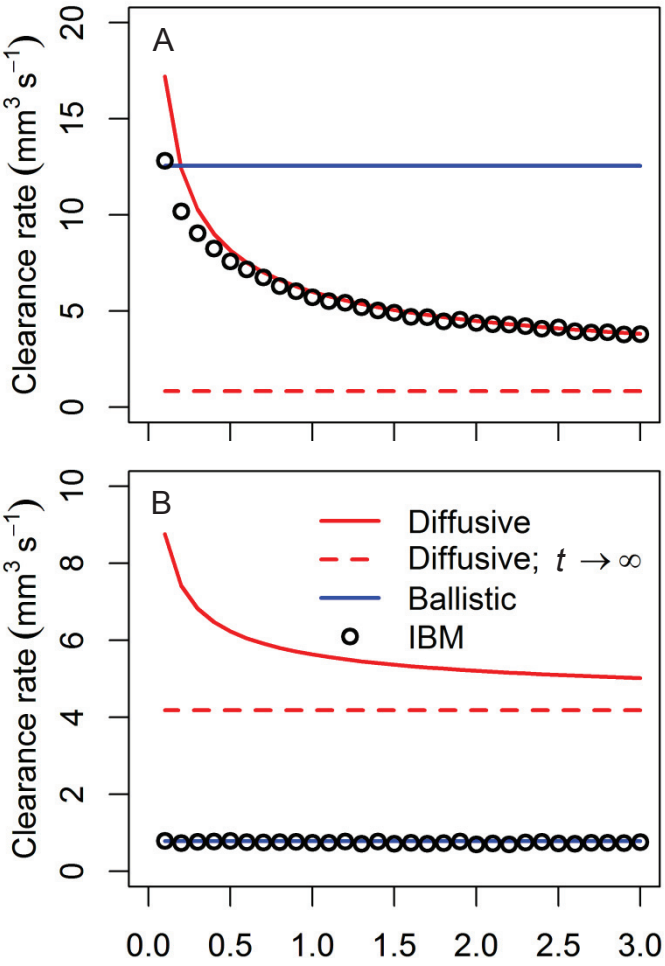

Figure 2.3: Time series of the realized maximum clearance rate from the IBM at high prey concentration (2.5 x 10^3 prey mm^{-3}) and solutions to the diffusive and ballistic models near the (A) "diffusive side" ($\lambda/r = 0.05$) and (B) "ballistic side" ($\lambda/r = 4$) of the diffusive to ballistic transition.

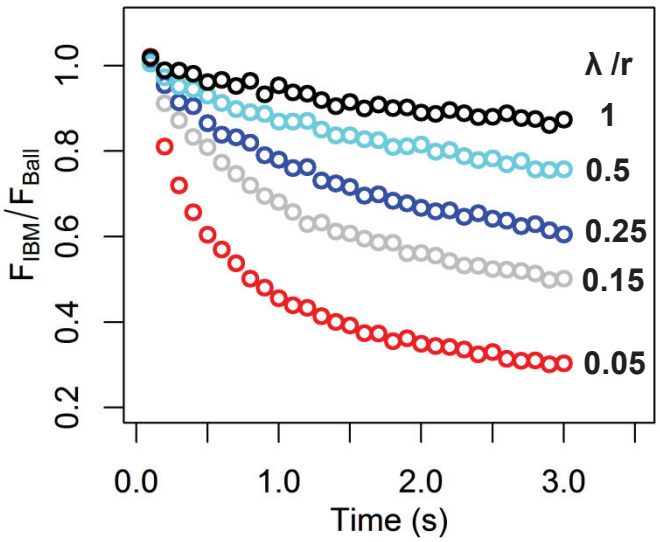

Figure 2.4: Time variation of mean F_{IBM}/F_{Ball} (n = 6 for each point) for r = 2 mm, and λ = 0.1 mm (red), 0.3 mm (grey), 0.5 mm (blue), 1 mm (cyan), and 2 mm (black).

indicated that the *Fuchs* (1964) and *Harris* (1982) corrections were inaccurate near the "ballistic side" of the diffusive to ballistic transition. The *Fuchs* (1964) correction appeared to plateau at a maximum value of $F/F_{Ball} < 1$, and the *Harris* (1982) correction decreased with increasing λ/r at $\lambda/r > \approx 4$ (Figure 2.6).

Values of F_{IBM}/F_{Ball} averaged over 3600 s were slightly higher than predicted by the *Visser* (2007) correction (Figures 2.5 and 2.7). Deviations from the *Visser* (2007) correction were highest at $\lambda/r \approx 1$. I expected that predictions from the IBM would overestimate the maximum clearance rate at steady state because F_{IBM} was time-averaged, and steady state is probably not reached within 3600 s for many values of λ/r. The *Visser* (2007) correction, which is a Michaelis-Menten model (Table A.1), can be easily tweaked to approximate the time-averaged data from the IBM by decreasing the half saturation constant. For example, decreasing the half saturation constant from 0.75 to 0.5 appeared to improve the fit of the *Visser* (2007) correction to F_{IBM}/F_{Ball} (Figure 2.7).

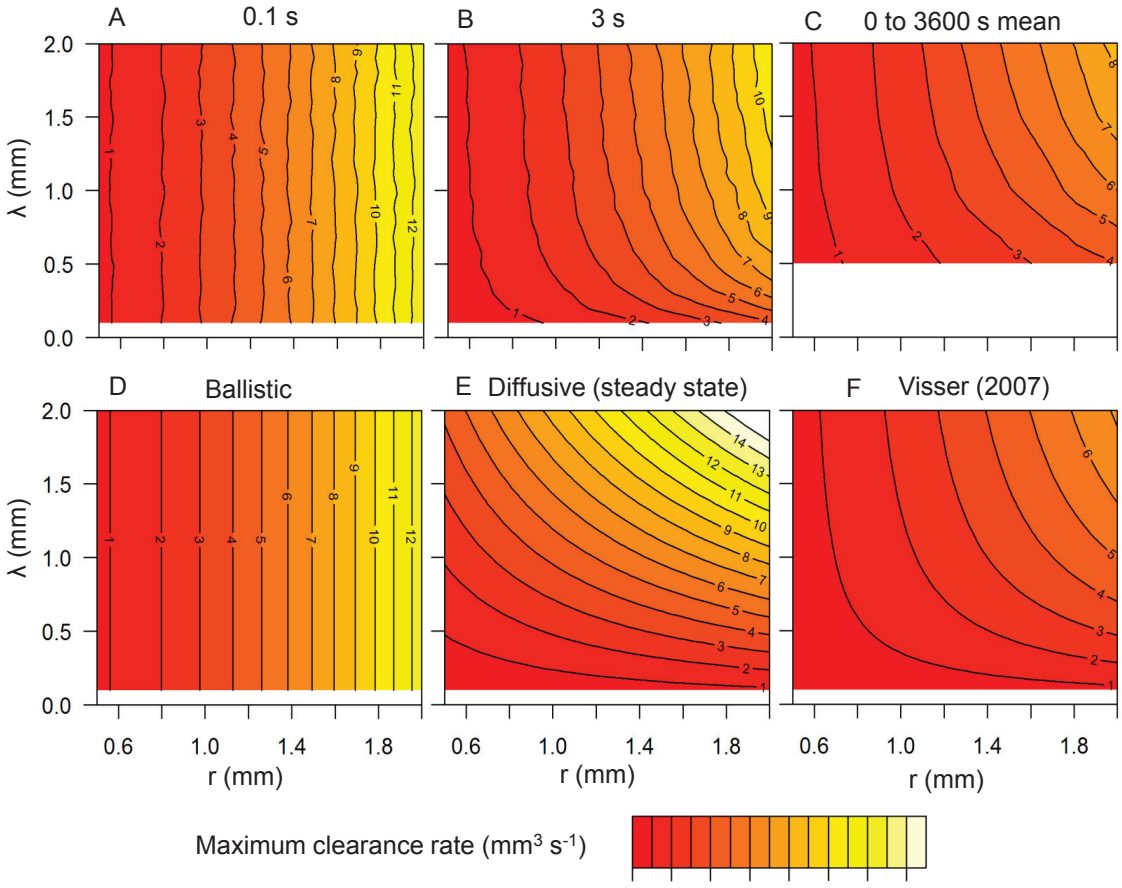

Figure 2.5: Surfaces of the maximum clearance rate (mm^3 s^{-1}) as a function of λ and r. Plots A and B represent mean F_{IBM} (n = 6) at 0.1 s and 3 s, respectively. Plot C represents mean F_{IBM} (n = 5), time averaged over 3600 s. Plots D, E, and F represent predictions from the ballistic model (Equation 2.3), diffusive model (at steady state; Equation 2.1), and *Visser* (2007) correction (see Table A.1 for formula), respectively.

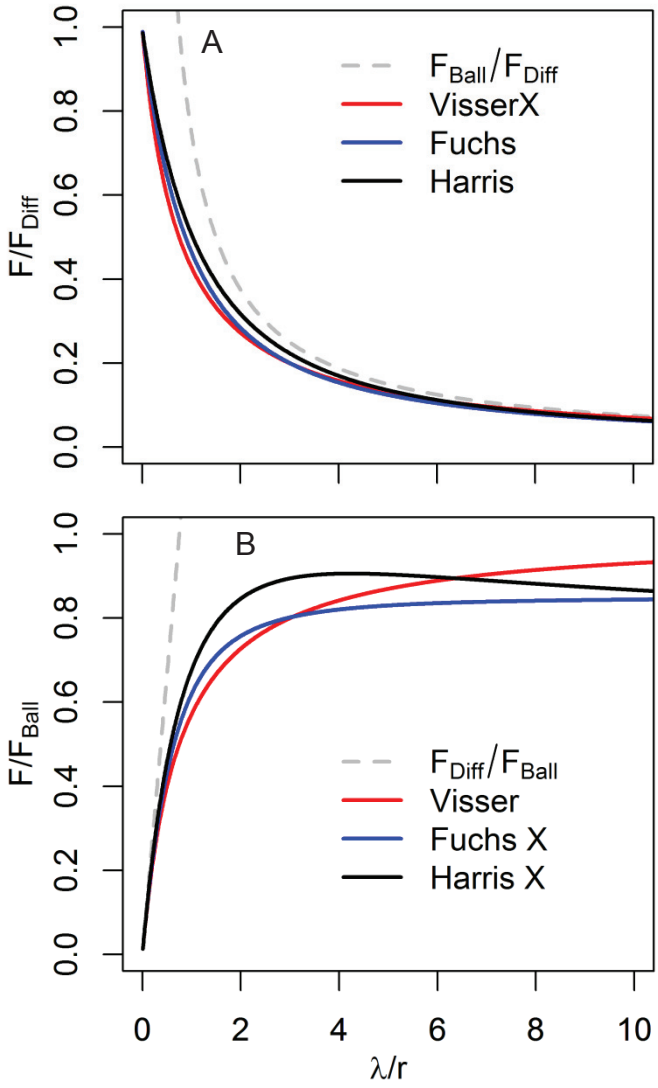

Figure 2.6: The relationship between λ/r and corrections to (A) the diffusive model; and (B) the ballistic model and λ/r. The *Visser* (2007) correction to the ballistic model was converted to a correction to the diffusive model by multiplying by the conversion factor, X = F_{Diff}/F_{Ball}. The *Fuchs* (1964) and *Harris* (1982) corrections to the diffusive model were converted to corrections to the ballistic model by multiplying by the conversion factor, X = F_{Ball}/F_{Diff} (see Table A.1 for formulae to corrections).

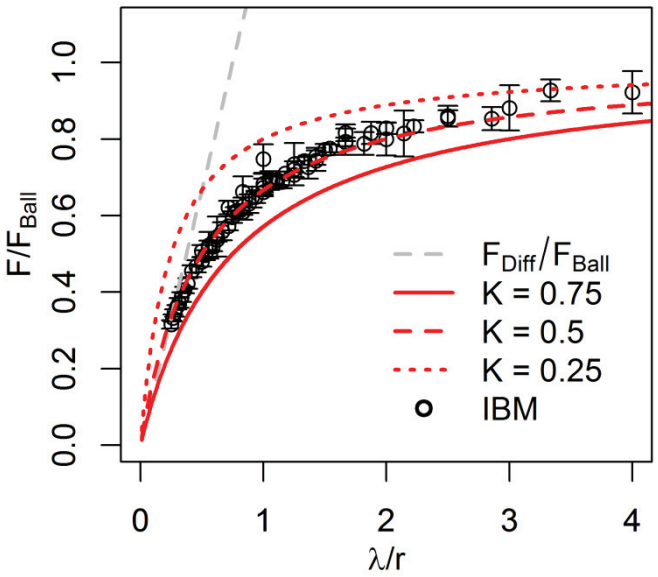

Figure 2.7: Relationships between λ/r and (1) mean $F_{IBM}/F_{Ball} \pm 95\%$ CI (n = 5), time-averaged over 3600 s; and (2) the *Visser* (2007) correction to the ballistic model, calculated with half saturation constants of K = 0.25, 0.50, and 0.75.

2.5 Discussion

2.5.1 Corrections to ballistic and diffusive models

The ballistic and diffusive models are valuable tools for the mechanistic prediction of encounter rates in the plankton. However, it is likely that many encounters between predator and prey are determined by the maximum clearance rates that occur over the transition from diffusive to ballistic movement (*Visser and Kiørboe*, 2006), which, to the best of my knowledge, have not been thoroughly described at scales relevant to zooplankton feeding. *Harris* (1982) stated that diffusive to ballistic transition occurs over a range of values of directional persistence (as perceived by the predator) on the order of $0.1 < \lambda/r < 10$. My results are generally consistent with this range. Because of the time variation in the maximum clearance rate, I emphasize that the time spent searching for prey is an important factor when considering use of a "classic" model or its correction. For example, I found that at $\lambda/r = 4$, time averaged F_{IBM} was consistent with F_{Ball} on the scale of seconds, but was slightly lower ($\approx 8\%$) than F_{Ball} after 1 h. Note that even small deviations in the maximum clearance rate can result in large differences in cumulative ingestion of prey if the concentration of prey is sufficiently high and the time spent searching for prey is

sufficiently long. The effect of time on the realized maximum clearance rate is further discussed in the following subsection.

Comparison of corrections to the diffusive and ballistic models indicated that the *Visser* (2007) correction is the most useful because it produced predictions that were similar to data that emerged from the IBM, and is the simplest equation to implement in larger models ($e.g.$, *Visser*, 2007). Also, because the *Visser* (2007) correction is a Michaelis-Menten model, its half saturation constant can be easily modified to predict time-averaged (non-steady state) values that emerge from the IBM. The *Fuchs* (1964) correction was most similar to that of *Visser* (2007). In fact, when $\lambda << r$, the *Fuchs* (1964) correction to the diffusive model also reduces to a Michaelis-Menten form (see *Fuchs*, 1964 and subsection A.1 in Appendix A). Both *Fuchs* (1964) and *Harris* (1982) acknowledged that their corrections to F_{Diff} are approximations. My analysis indicates that the *Fuchs* (1964) and *Harris* (1982) corrections are most appropriate near the "diffusive side" of the diffusive to ballistic transition ($i.e.$, when $\lambda/r <\approx 0.5$).

2.5.2 Time varying and steady state predictions

I have shown that the decrease in the maximum clearance rate with time is rapid and gradual when λ/r is small and large, respectively. Furthermore, the strength of the time dependence of the maximum clearance rate decreases non-linearly as λ/r increases. Time variation in the maximum clearance rate may not be ecologically important near opposing ends of the diffusive to ballistic transition because (1) steady state is approached rapidly when directional persistence is negligible ($e.g.$, steady state is reached over $\approx$ 2 minutes at λ/r = 0.05) and (2) the correction to F_{Ball} is small when directional persistence is substantial ($i.e.$, at λ/r = 10, the *Visser* (2007) correction is 0.93). This is consistent with my findings that that deviations from time-averaged maximum clearance rates over 1 h and steady-state predictions from the *Visser* (2007) correction were largest at intermediate values of λ/r.

It has been suggested that copepods can maintain clearance rates above steady-state by jumping to a new location, effectively re-setting depleted prey in their immediate vicinity to the far-field concentration (*Titelman and Kiørboe*, 2003). Jump frequencies of copepods measured in the laboratory range from 0.01 s^{-1} to 3 s^{-1} ($e.g.$, *Titelman and Kiørboe*, 2003; *Henriksen et al.*, 2007). The potential effect of jumping can be visualized in Figure 2.5. For example, if a predator with a detection distance of 1.4 mm feeding on prey with

a persistence length of 0.1 mm jumps after 3 s, it will "reset" its clearance rate from approximately 2 mm^3 s^{-1} (Figure 2.5B) to 6 mm^3 s^{-1} (Figure 2.5A). Prey concentration profiles that occur over the feeding interval between jumps ($e.g.$, Figure 2.2) could be used to measure the distance that must be travelled in each jump so that the copepod lands in a field of prey that has not been partially depleted, assuming no other predator was recently there.

The concentration of prey is an important factor to consider when assessing the ability of a feeding behaviour to exploit near-ballistic maximum clearance rates over relatively short time periods. Encounters are likely intermittent and sporadic events at natural prey concentrations. If the prey concentration is sufficiently low that very few or no prey are encountered over a time period that is much greater than the persistence time or time interval between jumps, time variation in the maximum clearance rate may not be important. For perspective, laboratory estimates of maximum clearance rates of ambush feeding copepods of the genus *Acartia* (feeding on ciliates) and *Oithona* (feeding on dinoflagellates) are approximately 8 ml h^{-1} and 0.4 ml h^{-1}, respectively (*Saiz and Kiørboe*, 1995; *Svensen and Kiørboe*, 2000). Applying these values to concentrations of microzooplankton (10 cells ml^{-1}) and nanozooplankton (10^3 cells ml^{-1}) that may be expected in the sea (*Fenchel*, 1988), gives an encounter rate on the order of 0.01 prey s^{-1}. I speculate that high prey concentrations are probably required for organisms to take advantage of clearance rates near F_{Ball} that occur on short time scales at the onset of feeding.

2.5.3 Model assumptions and applications

In my model, the predator is stationary and the prey move as correlated random walkers. Because the rate of search is dependent on the relative movement of predator and prey, the model is applicable to the scenario in which a "cruise feeding" predator is feeding on non-moving prey, in addition to the scenario in which an "ambush feeding" predator is feeding on motile prey.

Studies by *Svensen and Kiørboe* (2000) and *Saiz et al.* (2003) provide data on observed maximum clearance rates of ambush feeding copepods of the genus *Oithona*, the volume of water surrounding the antennules in which prey are detected, and the swimming speed of the prey. I used these data to compare observed maximum clearance rates to F_{Ball} and the *Visser* (2007) correction over the range of persistence lengths reported in the literature for dinoflagellates ($i.e.$, 0.1 mm $< \lambda <$ 1.0 mm; see Table 2.1). The mean maximum

clearance rate $\pm$ 95% CI reported by *Svensen and Kiørboe* (2000) and calculated from Table 1 in *Saiz et al.* (2003) are 0.42 $\pm$ 0.10 ml h^{-1} and 0.28 $\pm$ 0.06 ml h^{-1}, respectively. My corresponding estimates of F_{Ball} (0.41 ml h^{-1} and 0.26 ml h^{-1}) are in agreement with these data. When I applied the *Visser* (2007) correction, predictions of the maximum clearance rates were lower, and ranged from 0.12 ml h^{-1} to 0.33 ml h^{-1}, and 0.09 ml h^{-1} to 0.22 ml h^{-1}, respectively. Assuming that the data on prey detection and swimming speed are accurate, this example suggests that persistence lengths of dinoflagellates can be larger than 1 mm, which is consistent with observations of ballistic movement of dinoflagellates (in the vertical dimension) by *Schuech and Menden-Deuer* (2014). I found that the effect of the sinking speed of *Oithonia* sp. on the maximum clearance rates was negligible because it was approximately 4 times smaller than that of the prey (see *Gerritsen and Strickler*, 1977). Therefore, in this case, the problem can be reduced to the scenario of the predator being motionless.

There are several different scenarios in which the predator and prey may be moving, and methods for the calculation of the maximum clearance rate for each scenario have been proposed. If movement of both predator and prey is assumed either diffusive or ballistic, the maximum clearance rate can be calculated from the diffusive model (Equation 2.1), using a diffusion coefficient of, $D = D_{predator} + D_{prey}$ (*Chandrasekhar*, 1943), or the ballistic model (Equation 2.3) using a swimming speed of $s = (s^2_{predator} + s^2_{prey})^{0.5}$ (*Evans*, 1989). If the movement of the predator is ballistic and the movement of the prey is diffusive, the maximum clearance rate can be calculated from $F = F_{Diff}$Sh, where Sh is the Sherwood number (*Kiørboe*, 2008). The Sherwood number is the ratio of flux of prey into the predator due to advection and diffusion to the flux due only to diffusion (*Karp-Boss et al.*, 1996). Finally, *Fuchs* (1964) provides a correction to the diffusive model if the movement of both the predator and prey are characterized by the same persistence length (note that the *Fuchs* (1964) correction in the Appendix is adapted for movement of the prey only). A numerical modelling approach would be useful to evaluate the scenario in which both prey and predator are moving as correlated random walkers with different persistence lengths.

The incorporation of directional persistence of plankton movement into encounter rate models increases the scope of theory. However, run-and-tumble movement generated

by CRW is an oversimplification of the swimming behaviour of many planktonic organisms. While CRW may be an appropriate model for the movement of certain organisms (*e.g., Escherichia coli*; *Berg et al.*, 1972), this model is not applicable when swimming trajectories are spatially structured (*Bianco et al.*, 2014), or anisotropic ($e.g.$, *Schuech and Menden-Deuer*, 2014). Persistence lengths can be measured from non-random paths and anisotropic movement, but may lead to inaccurate predictions of the true maximum clearance rate.

The model is most applicable to situations in which predators are constantly searching for prey in homogenous environments on relatively small scales. Laboratory studies have demonstrated that zooplankton respond to environmental gradients by adjusting their swimming speed or path geometry to remain within favorable conditions, such as a patch of food (*Buskey*, 1984; *Verity*, 1991; *Woodson et al.*, 2005; *Menden-Deuer and Grünbaum*, 2006). Therefore, maximizing the rate of exploration of new environment (by using ballistic movement) is not necessarily advantageous because it may reduce the ingestion rate by facilitating an early exit from and environment enriched with prey.

The maximum clearance rate can be used to evaluate ingestion rates assuming that the predator is not satiated and that post encounter feeding efficiency is 100%. Prey within the detection distance of the predator may not be encountered if the predator is satiated. Satiation can be accounted for by implementing the maximum clearance rate as the "attack rate" in *Holling* (1959b)'s disk equation. Encountered prey may not be ingested because prey may escape. The ballistic model can be easily modified by multiplying F_{Ball} by the probability of ingestion after encounter ($e.g.$, *Hansson and Kiørboe*, 2006); however, this method cannot be used to adjust F_{Diff} (*Collins and Kimball*, 1949). *Fuchs* (1964) provides a formula for the inclusion of a feeding efficiency term in the correction to the diffusive model. This problem can be explored using an IBM by assigning prey with a probability to reflect off (or pass through) the predators encounter sphere, or disappear if the escape response of the prey results in movement far from the immediate vicinity of the predator.

2.6 Conclusions

In this study, I presented an individual based model (IBM) for the prediction of the maximum clearance rate of a motionless ($i.e.$, ambush feeding) predator from correlated

random walk (CRW) movement of prey. The model is also directly applicable to a moving ($i.e.$, cruise feeding) predator searching for motionless prey. My description of the maximum clearance rate over the transition from diffusive to ballistic prey movement illustrated that the diffusive and ballistic models can give overestimates if their assumptions of movement are not valid. I compared three corrections to classic "diffusive" and "ballistic" models, and argue that the correction proposed by *Visser* (2007) is the most useful because it was consistent with the simulated data and is the simplest correction to implement in larger models. The *Visser* (2007) correction can also be easily tweaked to non-steady state predictions from the IBM by modifying the half saturation constant. The latter is potentially important, given that non-steady state predictions may be relevant in scenarios in which the time spent searching for prey is shorter than the time to reach steady state. My work highlights the need for future studies on the potential interactions between the effect of directional persistence and concentration of prey, movement of both predator and prey, and feeding efficiency on rates of search, encounter, and ingestion.

CHAPTER 3

THE EFFECT OF TEMPERATURE ON MOTILITY OF THE NAUPLIUS AND CYPRIS STAGES OF THE ACORN BARNACLE, *Semibalanus balanoides*

3.1 Abstract

Variability in motility of planktonic larval marine benthic invertebrates with environmental conditions can affect the dispersal and survival of individuals by its influence on encounters with food and predators, horizontal transport, and settlement. I quantified swimming speed and directional persistence, expressed as a persistence time and persistence length ($i.e.$, run duration, and run length of a random walker), of nauplii and cyprids of the acorn barnacle, *Semibalanus balanoides*, over a temperature range of 0 to 12°C. I fit persistence time and length parameters in a correlated random walk model to displacement data obtained from video-recordings in 2D (horizontal and vertical dimensions). Nauplii (stages 2 and 6) were generally characterized by lower swimming speeds (nauplii: 0.98 to 2.54 mm s^{-1}, cyprids: 2.56 to 3.19 mm s^{-1}) and higher persistence times (nauplii: 1.18 to 5.49 s, cyprids: 0.29 to 0.92 s), and higher lengths (nauplii: 1.52 to 11.12 mm, cyprids: 0.96 to

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My coauthor Dr. Anna Metaxas supervised the study design and analysis, and edited the manuscript.

2.80 mm). Significant correlations between temperature and persistence length resulted from the effect of temperature on swimming speed for stage 6 nauplii and persistence time for cyprids. Analyses indicated directional bias of each swimming metric in the vertical dimension. Although the correlated random walk model is an idealized model of animal movement, I suggest that the quantification of directional persistence of larval marine benthic invertebrates can provide new insight into the evolutionary trade-offs associated with feeding and non-feeding life history strategies.

3.2 Introduction

Planktonic larvae of marine benthic invertebrates swim by movement of cilia or specialized appendages (*Chia et al.*, 1984). Larvae must swim to remain suspended in the water column, ingest food, avoid predation, and find suitable substrate for settlement. These factors affect larval survival, transport, and ultimately population connectivity (*Metaxas and Saunders*, 2009).

It is well established that animal behaviour often reflects a trade-off between searching for food or mates and avoiding predators (*Lima and Dill*, 1990). Models of the rates of random search and encounter facilitate the development of hypotheses regarding (1) the selective pressures of ingesting food and avoiding predators on motility traits ($e.g.$, *Visser and Kiørboe*, 2006), and (2) the consequence of these traits on the fitness of organisms (*Visser*, 2007), and dynamics of plankton communities (*Gerritsen and Strickler*, 1977; *Litchman et al.*, 2013). Zooplankton may increase their rate of random search for food by increasing their diffusivity at a cost of increasing the probability of swimming into a predator (*Visser and Kiørboe*, 2006).

Swimming speed and diffusivity are two examples of motility traits in models that predict the rate of random search and encounter assuming ballistic movement ($i.e.$, the magnitude of displacement is proportional to time), and diffusive movement ($i.e.$, the magnitude of displacement is proportional to time$^{0.5}$), respectively (*Kiørboe*, 2011). Directional persistence ($i.e.$, the tendency of a random walker to maintain directional of travel) is an additional trait that bridges the gap between ballistic and diffusive movement. In movement models known as "correlated random walk" (see *Codling et al.*, 2008), directional persistence is expressed as a correlation in direction between adjacent discrete movements, which can be used to derive a "persistence time" (*Taylor*, 1922). The persistence time is the

mean time of each "run" in discrete run and tumble movement, and is inversely related to the rate of change in direction of travel (*Taylor*, 1922; *Dunn*, 1983), and the corresponding "persistence length" is a product of the swimming speed and persistence time.

The persistence length influences predation risk, as higher persistence lengths result in a higher probability of encountering a predator (*Visser and Kiørboe*, 2006). Studies that quantify swimming metrics that influence predation risk can provide new insights into classic concepts in larval ecology. For example, planktotrophy is often associated with a high reproductive output and low parental investment of energy per offspring, at the cost of an extended larval duration over which integrated losses to mortality are potentially significant (*Strathmann*, 1985). An additional cost may be that planktotrophic larvae are inherently more vulnerable to encounters with predators due to their requirement to search for food.

Both the directional persistence and swimming speed determine the diffusivity of a random walker, and therefore influence the rate of search for food, and the distribution of organisms. Planktonic ciliates and dinoflagellates have been shown to decrease their swimming speed and rate of turning ($i.e.$, directional persistence) in response to favorable environmental conditions, such as a patch of food, which results in the aggregation of individuals in space ($e.g.$, *Buskey and Stoecker*, 1988; *Menden-Deuer and Grünbaum*, 2006). Although this behaviour reduces the diffusivity of grazers and their rate of search for food, it can actually enhance their growth rate because foraging occurs at a relatively high concentration of prey (*Menden-Deuer and Grünbaum*, 2006).

In this study, I quantified the variability in swimming speed, persistence time, and persistence length of larvae of the acorn barnacle, *Semibalanus balanoides*, over a range of temperatures experienced during their larval duration in the Northwest Atlantic. The larvae progress through six naupliar stages and a cypris stage (*Crisp*, 1962) over a period of several weeks (*Bousfield*, 1954). Swimming serves several important functions for larval barnacles. In the naupliar stages, feeding is dependent on swimming because nauplii use their appendages to swim and collect food simultaneously (*Walker et al.*, 1987; *Anderson*, 1994). Swimming in the vertical dimension can indirectly affect horizontal advection of both nauplii and cyprids by ocean currents ($e.g.$, *Bousfield*, 1955; *Shanks and Wright*, 1987) and influence the vertical distribution of settlers (*Grosberg*, 1982).

I expected that temperature would increase larval swimming speeds as a result of a

decrease in viscosity and increase in the rate of biochemical reactions (*Larsen and Riisgård*, 2009), and therefore increase persistence length. Nauplii feed by action of their swimming appendages, whereas the cyprids are non-feeding and adapted for settlement (*Walker et al.*, 1987; *Anderson*, 1994). The nauplii must feed to build energy reserves that are required for the settlement and metamorphosis of the cypris stage (*Lucas et al.*, 1979); therefore, I expected their persistence length to be higher than that of cyprids.

3.3 Methods

3.3.1 Adult collection and larval rearing

I collected individuals of adult *Semibalanus balanoides* from Northwest Arm in Halifax, NS, in winter 2014 and 2015 (Table 3.1), transported them to the Dalhousie University Aquatron facility, and held them in continuously flowing seawater at ambient temperature, which ranged from 2 to 4°C. After 1 to 2 days, I induced release of larval barnacles by feeding adults diatoms (*Thalassiosira weissflogii*) in a closed container for 3 to 4 h; over this time period, I allowed the temperature to rise from ambient to 12°C. Immediately after larval release, I transferred the larvae into 4-l glass culture jars containing 3 l of 1-μm filtered seawater at 6°C and maintained larvae in culture until the second nauplius (N2), sixth nauplius (70-90% of individuals in sixth stage, N6), or cypris stage was reached for experimentation. I replenished seawater and algal food (3 to 1 mixture of *T. weissflogii* and *Isochrysis* sp. at a combined concentration of 10^5 cells ml^{-1}) every other day.

Table 3.1: Methodological details regarding the collection of adult *Semibalanus balanoides*, larval culture, and experimentation. A separate experiment was conducted for each stage, using larvae from a different set of adults.

Stage	Date of collection	Culture duration to stage (d)	Acclimation period (h)	Observation period (h)
N2	12 March 2014	1	4 to 7	10
N6	17 February 2014	15	6 to 14	12
Cypris	9 March 2015	19	7 to 10	10

3.3.2 Experimental set-up and design

I video-recorded 2D larval swimming trajectories (in horizontal, x, and vertical, z, dimensions) with a Nikon D5100 digital camera (frame rate: 30 fps) oriented perpendicular to a

10 x 10 x 10-cm arena in a plexiglass column, in which I added 1 l of 1-μm filtered seawater and larvae at a concentration of 0.5 to 0.7 individuals ml^{-1}. Because swimming behaviour of larval barnacles is sensitive to light (*Crisp and Ritz*, 1973), I did the experiments in darkness with an infrared illumination source (wavelength: 850 nm) positioned on the side of the column opposite to that of the camera.

I video-recorded larvae swimming at 0, 3, 6, 9, and 12°C ($\pm$ 1°C) in separate experiments for each stage (Table 3.1). These temperatures represent the thermal range experienced by larval *S. balanoides* in NW Atlantic (*Pineda et al.*, 2002; *Sorochan and Metaxas*, 2015). In each experiment, I obtained 3 to 5 video-recordings per temperature. Prior to capturing videos, I placed the larvae in 4-l jars containing 1 l of 1-μm filtered seawater, and immersed the jars in flowing seawater at a temperature corresponding to each treatment. I staggered the time over which groups of 4 to 5 jars with randomly assigned temperatures were transferred into their corresponding tanks, resulting in an acclimation period that ranged from 4 to 14 h (Table 3.1).

To obtain a video-recording, I transferred larvae from a jar into the column, waited 2 min to allow turbulence to dissipate and larvae to adjust to the new vessel, and recorded larval trajectories for 5 min. After each video-recording, I preserved larvae in 95% ethanol for identification of larval stages, and thoroughly rinsed the column. All observations from all temperatures were completed over 10 to 12 h. To prevent warming of the seawater during each observation, I ran seawater at the corresponding temperature treatment through a water jacket around the exterior of the column. The coldest seawater available to run through the water jacket was 3°C; therefore, this temperature was used in the water jacket for the 0°C treatment. The seawater temperature warmed by up to 1°C for all temperature treatments, except for the 0°C treatment, which warmed to 2°C. I estimated the actual temperature experienced by the larvae as the average of the initial and final temperatures.

3.3.3 Data collection

I extracted images at 0.25-s intervals from each video, and converted each image into a binary format such that each larva in an image was represented as a group of white pixels on a black background. I used particle tracking software (*Blaire and Dufresne*, 2008) to determine larval co-ordinates (x, z) from the centroid of each pixel group, and identify paths based on the location of larval positions between successive frames. The raw data were processed manually to remove artificial paths caused by sinking aggregates of algae

or molts that were introduced when larvae were transferred to the container in which they were acclimated. I also manually annealed path segments (separated by a time interval < 1 s) that were assigned different paths by the tracking algorithm, but belonged to the same larva. This occurred when larvae moved in and out of focus. To convert pixels to travel distances, I measured the number of pixels corresponding to a distance of 1 cm from an image of a ruler immersed in the column in the plane of focus using Image J software.

I used path duration of 6 s to maximize the number of paths that could be analyzed from each video (Figure 3.1). For each path, I estimated the mean swimming speed, $\bar{s}$, and maximum swimming speed, s_{max}. These variables were then averaged over all paths to obtain a single estimate from each video-recording. The value of s_{max} was evaluated in addition to $\bar{s}$ because the effect of temperature on the former is sometimes greater than on the latter ($e.g.$, *Moison et al.*, 2012). Both swimming speed metrics were quantified in the xz plane, as well as the x and z dimensions. I also measured the mean ratio of net displacement to gross distance travelled, NGDR, after 6 s in the vertical and horizontal dimension to determine if larval trajectories were biased in direction of travel within each video recording.

I quantified swimming metrics from 2D projections (in the xz plane) of 3D trajectories. My results are therefore comparable to those from other studies that have quantified swimming speeds and directional persistence from trajectories of plankton collected in 2D (*Kiørboe et al.*, 2004; *Kiørboe and Bagøien*, 2005; *Visser and Kiørboe*, 2006). It is well documented swimming speeds are underestimated when derived from observations in 2D (*Kiørboe and Bagøien*, 2005; *Dur et al.*, 2011). Also, I suspect that my observations in 2D were biased towards slow and convoluted movement (resulting in underestimates of swimming speed and directional persistence), as rapid and sustained movement in the y dimension (which was not observed) would result in larvae quickly moving out of the plane of focus.

Despite these problems, I am confident that there was no interaction between the biases associated with 2D measurements and the potential effect of temperature on the larval motility metrics used in this study. This would occur if there was an interaction between temperature and directional bias in swimming metrics in the horizontal ($i.e.$, xy) plane. It is unlikely that the direction of travel was biased in the horizontal plane, where environmental

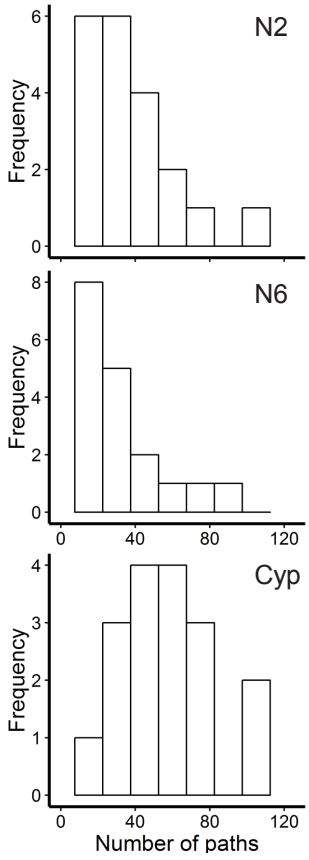

Figure 3.1: The distribution of the number of larval swimming paths sampled per video-recording for the following Stages: (A) second nauplius (N2); $8 \leq n \leq 87$, (B) sixth nauplius (N6); $10 \leq n \leq 98$, and (C) cypris (Cyp); $20 \leq n \leq 124$.

conditions were uniform. I believe zooplankon are more likely to exhibit temperature-dependent directional biases in the vertical dimension due to potential interacting effects of temperature and pressure on swimming behaviour.

3.3.4 Estimation of directional persistence from random walk

I used a correlated random walk model to estimate the persistence time, τ, and persistence length, $\lambda = \tau s$, where s is the swimming speed. Correlated random walk assumes larvae move at a constant s, and the direction of travel is globally unbiased, but correlated at small time scales between successive movements (*Taylor*, 1922; *Codling et al.*, 2008). I estimated these metrics from larval movements in the xz plane. I conducted separate analyses in the x and z dimensions to evaluate potential directional bias in movement ($e.g.$, *Schuech and Menden-Deuer*, 2014).

The root mean squared distance traveled, l, of a correlated random walker is expressed in terms of s, τ, and time, t, as:

$$l = s(2\tau(t - \tau(1 - e^{-t/\tau})))^{0.5} \tag{3.1}$$

Equation 3.1 was derived by *Taylor* (1922) in 1D, and by *Dunn* (1983) in 2D. Estimates of τ and s can be obtained by fitting the parameters in Equation 3.1 using non-linear regression (*Dunn*, 1983). This method has been used to characterize the motility of planktonic organisms (*Kiørboe and Bagøien*, 2005; *Visser and Kiørboe*, 2006; *Schuech and Menden-Deuer*, 2014).

Equation 3.1 can be expressed in terms of the ratio of the root mean squared distance travelled to the gross distance travelled, l/L:

$$\frac{l}{L} = (2(\eta - \eta^2(1 - e^{-1/\eta})))^{0.5} \tag{3.2}$$

where $\eta = \tau/t = \lambda/L$, and $L = st$. Because s was not constant in my data, I approximated L by computing the mean integrated distance travelled at each t. In preliminary analyses, I found that fitting τ to both Equation 3.1 and Equation 3.2 produced similar results, but there was less variability when τ was fit to Equation 3.2. Therefore, I estimated τ and λ separately by fitting these parameters to Equation 3.2.

3.3.5 Statistical analysis

I used the Spearman rank correlation coefficient, ρ, to evaluate the relationship between temperature and each of the swimming metrics $\bar{s}$, $\bar{s}_{max}$, τ, and λ quantified from xz plane. Separate analyses were conducted for each stage. For $\bar{s}$ and $\bar{s}_{max}$, I tested the null hypothesis that $\rho \leq 0$, and for all other metrics I tested the null hypothesis that $\rho = 0$. The significance of ρ was determined using critical values obtained from *Zar* (1999).

I used sign tests and Spearman correlations to test for bias in motility in the x and z direction, and the interaction between directional bias and temperature, respectively. Specifically, I used the sign test to evaluate the null hypothesis of no difference between z and x components of each swimming metric ($\bar{s}$, $\bar{s}_{max}$, τ, and λ), and used Spearman correlations to evaluate the null hypothesis that $\rho = 0$. Both tests were also conducted on the NGDR in the horizontal and vertical dimensions to test the null hypotheses of no difference in the direction of travel after 6 s, and that $\rho = 0$.

The number of larval paths used to quantify swimming metrics varied substantially among video-recordings in each experiment (Figure 3.1). To evaluate the potential effect of this additional source of variability on stage-specific relationships between each swimming metric and temperature, I carried out separate correlation analyses using 100 subsets of randomly sampled paths within each video-recording. The number of paths in each subset was the minimum number of paths observed among all videos for each stage (n = 8, 10, and 20 paths per subset for stages N2, N6, and cypris stages, respectively). All analyses were conducted using R v 3.3.1.

3.4 Results

The paths of nauplii were characterized by arcs or meandering loops, whereas those of cyprids were often characterized by convoluted zig-zags resulting from periods of forward movement and passive sinking (Figure 3.2). Cyprids generally exhibited lower values of l/L than nauplii, especially in the vertical dimension (Figure 3.3). Values of l/L often deviated from the expectation of correlated random walk over the transition from ballistic to diffusive movement. As τ/t decreased, l/L converged on the expectation from CRW and diffusion (Figure 3.3). I have not shown the relationship between l/L and λ/L as it was similar to that of l/L and τ/t. See Figures B.1, B.2, and B.3 for curve fits to Equation 3.2 (for τ_{xz}) for each video-recording.

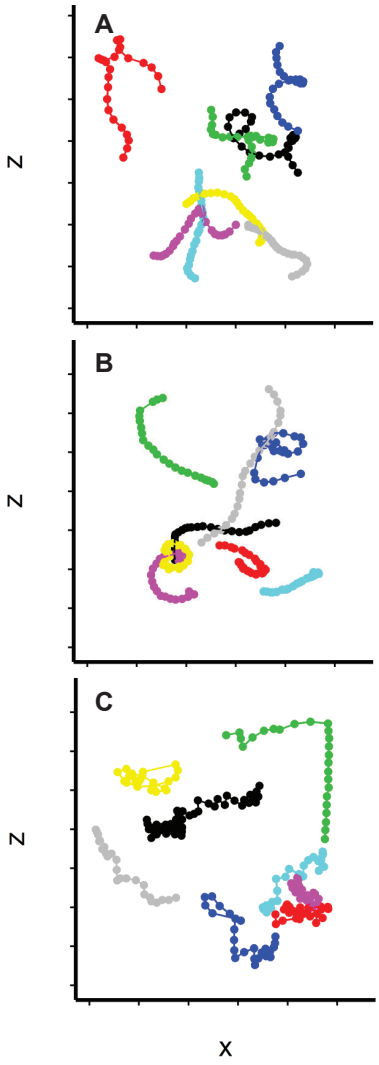

Figure 3.2: Examples of swimming paths of the (A) second nauplius and (B) sixth nauplius and (C) cypris stages over 6 s. Tick marks on the axes correspond to increments of 4 mm.

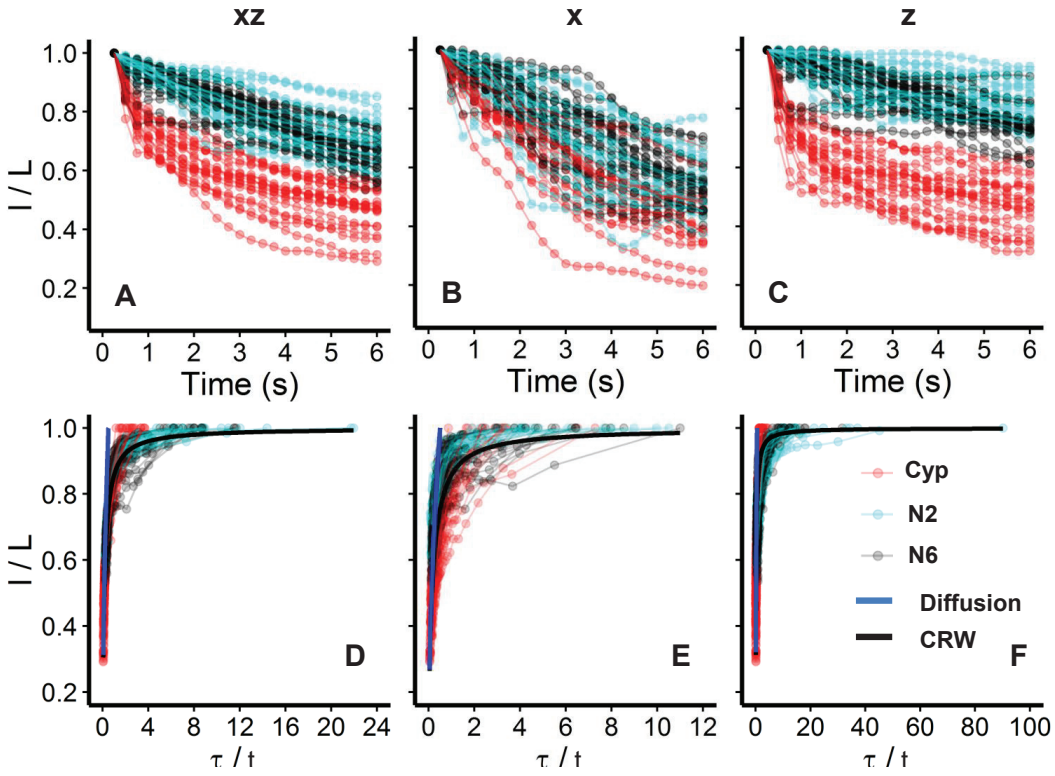

Figure 3.3: Relationships between the ratio of the root mean squared distance to gross distance travelled, l/L, and time, t is shown in the upper panels in (A) 2D, (B) the horizontal dimension, and (C) the vertical dimension. Relationships in (A to C) were used to fit the persistence time, τ, in Equation 3.2. Relationships between l/L and τ/t are shown in the lower panels in (D) 2D, (E) the horizontal dimension, and (F) the vertical dimension. In all figures, each line represents data from a single video-recording of the second nauplius (N2), sixth nauplius (N6), or cypris (cyp). In (D-F), the blue and black lines indicate the expected relationship from diffusion and correlation random walk (CRW) models, respectively.

Correlation analyses on movement data in the xz plane using all available paths from each video-recording indicated that both τ and λ of the cypris stage were negatively correlated with temperature (Figure 3.4, Table 3.2). A significant negative correlation between τ and temperature was detected for the second nauplius (N2), whereas a significant positive correlation between λ and temperature was detected for the sixth nauplius (N6; Figure 3.4, Table 3.2). Significant correlations between $\bar{s}$ and temperature were only detected for nauplii; however $\bar{s}_{max}$ and temperature were significantly positively correlated for all larval stages (Figure 3.5, Table 3.2).

Sign tests indicated a significant difference in the magnitude of each swimming metric between the vertical (z) and horizontal (x) dimensions, except for τ for cyprids and $\bar{s}_{max}$ for N6 (Figure 3.4; Figure 3.5; Table 3.3). Significant positive correlations between $\tau_z - \tau_x$ and $\lambda_z - \lambda_x$ and temperature were detected for N6 (Figure 3.4; Table 3.3). A significant negative correlation between NGDR_z and temperature was detected for cyprid larvae. There was no consistent vertical or horizontal directional bias on NGDR across the range of temperatures for any stage (Figure 3.6; Table 3.3).

When significant correlations were detected from all available paths, mean values of ρ from path subsets were usually lower and were only significant for $\bar{s}$ and $\bar{s}_{max}$ (Table 3.2, Table 3.3, Figures B.4 and B.5). Evaluation of the potential effect of sample size on $\tau_z - \tau_x$ and $\lambda_z - \lambda_x$ was not possible because the non-linear regression failed to fit curves to data from all random subsets at low sample sizes in the x and z dimensions.

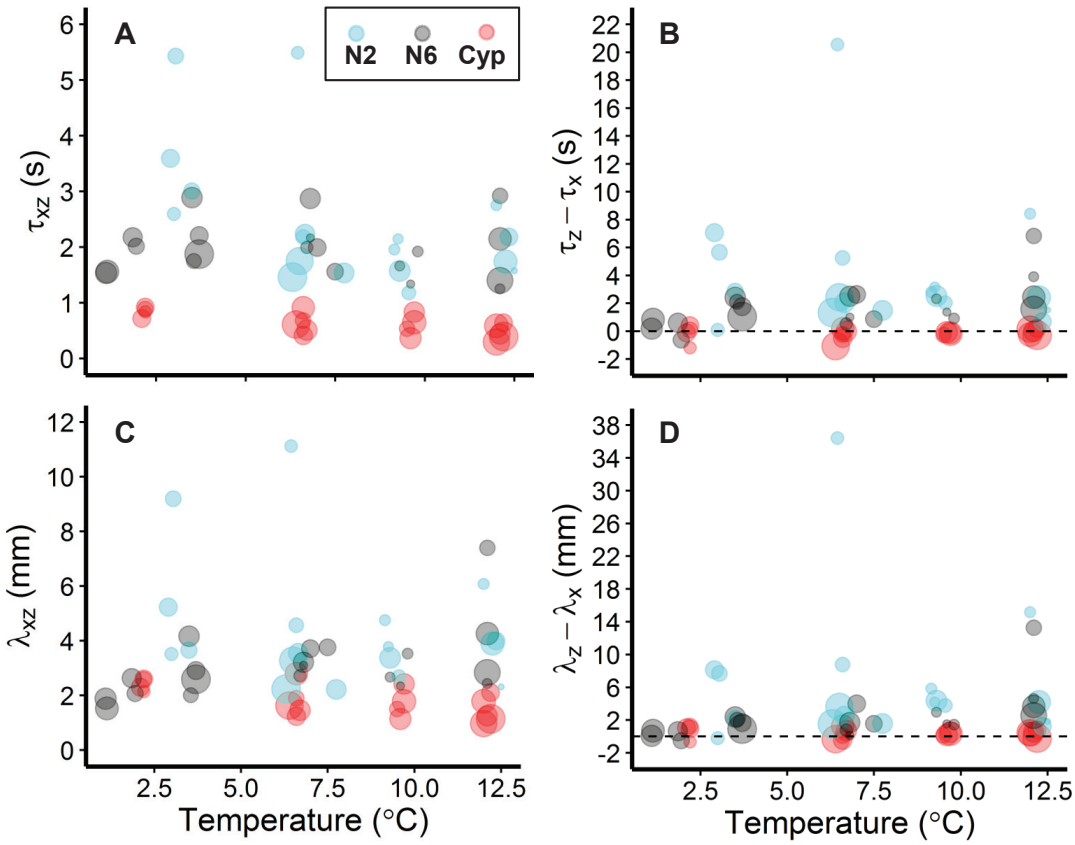

Figure 3.4: Relationships between temperature and (A) persistence time in 2D, τ_{xz}; (B) the difference between τ in the z and x dimension, $\tau_z - \tau_x$; (C) persistence length in 2D, λ_{xz}; and (D) the difference between λ in the z and x dimension, $\lambda_z - \lambda_x$. The size of each point is proportional to the ratio of the number of larval swimming paths used to estimate the metric of interest to the maximum number of paths observed within each stage. Stage 2 nauplius (N2); Stage 6 nauplius (N6); cypris (Cyp).

Table 3.2: Spearman rank correlation coefficients, ρ, from relationships between swimming metrics and temperature. Values of ρ are reported from relationships in which all paths were used. Mean values of ρ are reported from relationships of 100 path subsets (see Figure B.4). Cases in which $|\rho| > |\rho_{critical}|$ at $\alpha = 0.05$ are indicated in bold. Critical values, $|\rho_{critical}|$, for 1-sided tests for the second nauplius (N2) and Cypris (n = 18), and the sixth nauplius (N6; n = 20), were 0.401 and 0.380, respectively. Corresponding values of $|\rho_{critical}|$ for two-sided tests were 0.472 and 0.447, respectively.

Metric	**Larval stage**	ρ **all paths**	ρ **subsets**
$\bar{s}_{xz}$	N2	**0.577**	**0.484**
	N6	**0.841**	**0.827**
	Cypris	0.341	0.207
$\bar{s}_{max_{xz}}$	N2	**0.612**	**0.507**
	N6	**0.746**	**0.742**
	Cypris	**0.708**	**0.533**
τ_{xz}	N2	**-0.517**	-0.442
	N6	-0.164	-0.090
	Cypris	**-0.606**	-0.365
λ_{xz}	N2	-0.181	-0.226
	N6	**0.533**	0.367
	Cypris	**-0.526**	-0.327

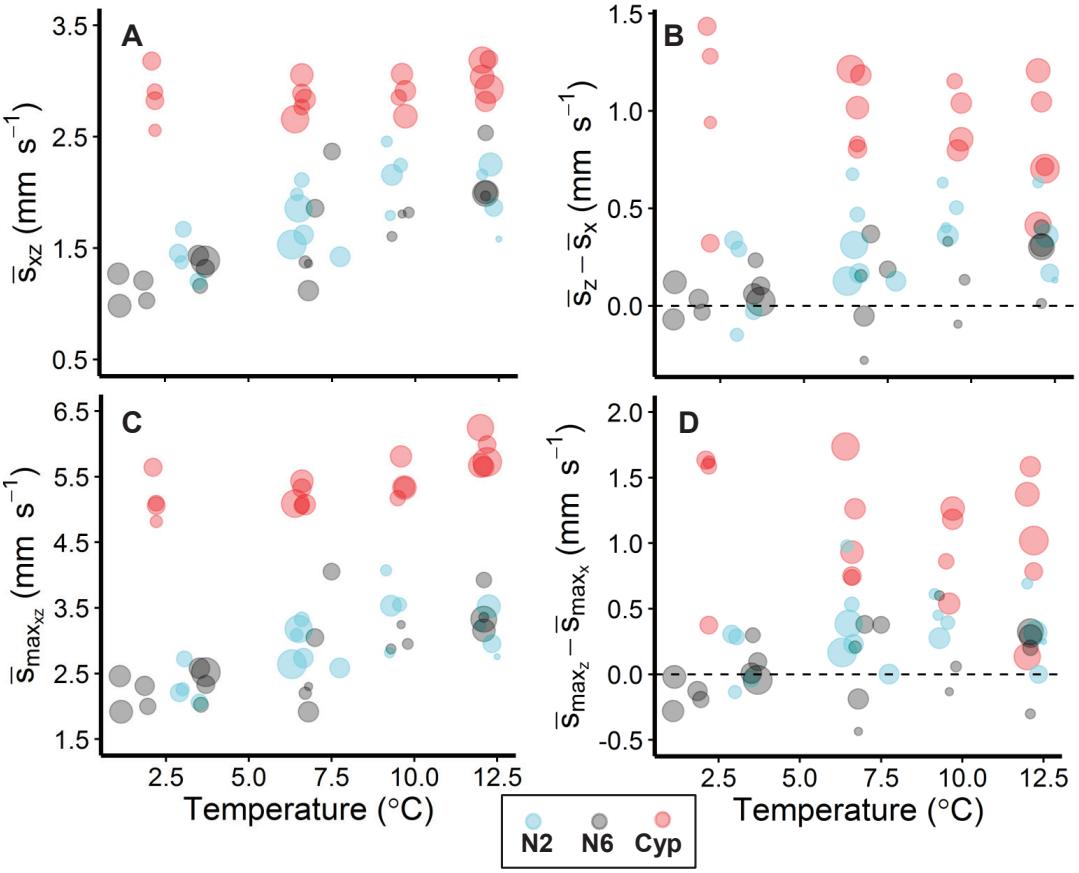

Figure 3.5: Relationships between temperature and (A) mean swimming speed in 2D, $\bar{s}_{xz}$; and (B) the differences between estimates of $\bar{s}$ in the z and x dimension, $\bar{s}_z - \bar{s}_x$; (C) maximum swimming speed in 2D, $\bar{s}_{max_{xz}}$, ; and (D) the difference between estimates of $\bar{s}_{max}$ in the z and x dimension, $\bar{s}_{max_z} - \bar{s}_{max_x}$. The size of each point is proportional to the ratio of the number of larval swimming paths used to estimate the metric of interest to the maximum number of paths observed within each stage. Stage 2 nauplius (N2); Stage 6 nauplius (N6); cypris (Cyp).

Table 3.3: Results from Spearman rank correlations and sign tests, used to evaluate directional bias in movement, and the interaction between directional bias and temperature, respectively. Values of ρ are reported from relationships in which all paths were used, and mean values of ρ are reported from relationships of 100 path subsets (See Figure B.5). Cases in which $|\rho| > |\rho_{critical}|$ at $\alpha = 0.05$ are indicated in bold. Critical values, $|\rho_{critical}|$ for the second nauplius (N2) and Cypris (n = 18), and the sixth nauplius (N6; n = 20), were 0.472 and 0.447, respectively. For the sign test, a "success" refers to a positive value of the swimming metric and a "trial" refers to the sample size, n, corresponding to each video recording.

		– Spearman correlation –		——— Sign test ———	
Metric	**Larval stage**	ρ **all paths**	ρ **subsets**	**Successes, trials**	**P-value**
$\bar{s}_z - \bar{s}_x$	N2	0.298	0.205	16, 18	$<$ **0.01**
	N6	0.410	0.306	15,20	**0.04**
	Cypris	-0.363	-0.264	18, 18	$<$ **0.01**
$\bar{s}_{max_z} - \bar{s}_{max_x}$	N2	0.189	0.126	15, 18	$<$ **0.01**
	N6	0.326	0.252	11, 20	0.82
	Cypris	-0.276	-0.219	18, 18	$<$ **0.01**
$\tau_z - \tau_x$	N2	-0.226	–	18, 18	$<$ **0.01**
	N6	**0.598**	–	–	–
	Cypris	0.115	–	5, 18	0.10
$\lambda_z - \lambda_x$	N2	-0.065	–	17, 18	$<$ **0.01**
	N6	**0.699**	–	–	–
	Cypris	-0.010	–	14, 18	**0.03**
NGDR_x	N2	-0.181	-0.109	5, 18	0.10
	N6	-0.233	-0.173	6, 20	0.12
	Cypris	-0.085	-0.084	9, 18	1
NGDR_z	N2	-0.098	-0.101	12, 18	0.23
	N6	-0.168	-0.135	9, 20	0.82
	Cypris	**-0.533**	-0.418	–	–

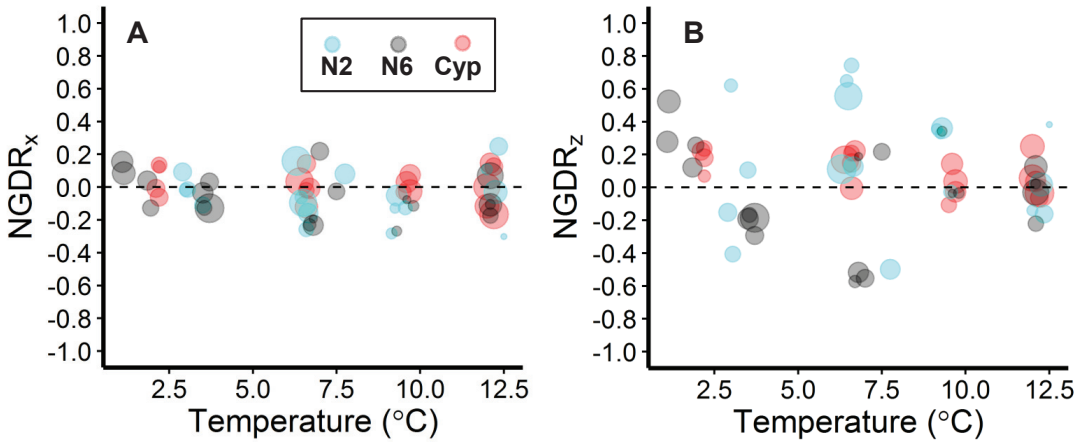

Figure 3.6: Relationships between temperature and the (A) ratio of net displacement to gross distance travelled in the x dimension, NGDR$_x$; and (B) the same ratio in the z dimension, NGDR$_z$. The size of each point is proportional to the ratio of the number of larval swimming paths used to estimate the metric of interest to the maximum number of paths observed within each stage. Stage 2 nauplius (N2); Stage 6 nauplius (N6); cypris (Cyp).

3.5 Discussion

3.5.1 Swimming speed in 2D

The range of the mean swimming speeds of nauplii (both N2 and N6) of *Semibalanus balanoides* was consistent with that of the second nauplius of *Amphibalanus improvisus* ($\approx$ 1 to 2.5 mm s^{-1}) observed in 2D (*Lang et al.*, 1980). The maximum swimming speed of nauplii that I observed was consistent with the swimming speed of the nauplii of *S. balanoides* challenged with flow ($\approx$ 4 mm s^{-1}, *Singarajah*, 1969). It is well established that barnacle nauplii are weaker swimmers than cyprids (*Walker et al.*, 1987; *Walker*, 2004). The exceptional swimming ability of cyprids is attributed to their six thoracic appendages and streamlined shape, which generate propulsion and reduce drag, respectively (*Walker et al.*, 1987). My observations of the mean speeds of cyprids were also consistent with reports of movement (sinking and swimming) of *S. balanoides* in still water wherein the majority of individuals travelled at speeds well below 10 mm s^{-1} (*DiBacco et al.*, 2011). Although averaged maximum swimming speeds of cyprids were the highest observed in my study, they do not represent the true swimming ability, as cyprids of *S. balanoides* can

swim at speeds > 70 mm s^{-1} (*DiBacco et al.*, 2011).

Temperature can affect the swimming speed of zooplankton by its influence on the physiology of organisms and viscosity of seawater, and both the biological and physical effects of temperature can be substantial (*Larsen and Riisgård*, 2009). *Yule* (1984) demonstrated that the swimming activity ($i.e.$, beat frequency) of the swimming appendages of nauplii of *S. balanoides* increased with temperature up to 25°C. Swimming speed has been shown to increase with temperature for many different zooplankton taxa, including the larvae of sea urchins (*Podolsky and Emlet*, 1993), bivalves (*Hidu and Haskin*, 1978), and decapods (*Sulkin et al.*, 1980), as well as adult copepods, (*Larsen et al.*, 2008; *Moison et al.*, 2012; *Svetlichny et al.*, 2017) and amphipods (*Lindström and Fortelius*, 2001).

Cyprids were able to compensate for temperature effects to maintain a constant mean swimming speed over the experimental range of temperatures. The absence of an effect of temperature on mean swimming speed has been observed in other crustaceans with strong swimming ability, including *Daphnia* sp. ($\approx$7 mm s^{-1}, *Gorski and Dodson*, 1996) and several species of copepods ($\approx$10 mm s^{-1}, *Hirche*, 1987). I expect that the effect of temperature on the swimming speed of cyprids will be largest near the upper limit of swimming ability. This may in part explain the slight increase of the maximum swimming speed with increasing temperature in my study; however, a true evaluation of swimming ability would require individuals to be challenged with flow (*DiBacco et al.*, 2011).

3.5.2 Directional persistence in *xz* plane

The magnitude of persistence lengths of both nauplii and cyprids across all temperatures in my study (median $\pm$ IQR of N2, N6, and cypris larval stages: 3.7 ± 1.4 mm, 2.8 ± 1.2 mm, 1.8 ± 1.0 mm) was similar to that reported for copepods (on the order of 1 to 10 mm; *Kiørboe and Bagøien*, 2005, *Visser and Kiørboe*, 2006, *Bianco et al.*, 2014). In a survey of plankton, *Visser and Kiørboe* (2006) found that the persistence length (measured in 2D) is roughly one order of magnitude larger than the corresponding equivalent spherical diameter (ESD). I do not have estimates of the ESD for larval *S. balanoides*; however, the biovolume of nauplii and cyprids from a different species, *Balanus crenatus*, has been estimated at ≈ 0.1 mm^3 (*Matsuno et al.*, 2012), with an equivalent spherical diameter (ESD) of ≈ 0.6 mm. Assuming *B. crenatus* and *S. balanoides* have similar biovolumes, the ratio of the median persistence length and ESD is generally consistent with the relationship described by *Visser and Kiørboe* (2006).

The persistence length is the product of the persistence time and swimming speed ($i.e.$, $\lambda = \tau s$). Correlations that I observed between persistence length of larval barnacles and temperature resulted from a different mechanism in each larval stage. With respect to the second nauplius (N2), the persistence length was not correlated with temperature, due to an offset between increasing swimming speed and decrease persistence time with increasing temperature. In contrast, the persistence length of the sixth nauplius (N6) was positively correlated with temperature due to an increase in swimming speed and no change in persistence time with temperature. Finally, the persistence length of the cypris stage was negatively correlated with temperature due to a decrease in persistence time and no change in swimming speed with temperature.

Ontogenetic variability in swimming behaviour is suspected to contribute to the variability in the vertical distribution of larval stages of crustaceans observed in the field ($e.g.$, *Bousfield*, 1955; *Queiroga and Blanton*, 2004). Temperature has been shown to play an important role in the stage-specific vertical distribution of larvae in laboratory experiments (*Ouellet and Allard*, 2006; *Daigle and Metaxas*, 2011, 2012). I did not evaluate the effect of temperature on the vertical distribution of individuals; however, my results indicate that cyprids lower their rate of spreading ($i.e.$, $D \propto s^2\tau$) with increasing temperature by decreasing their persistence time and maintaining a constant swimming speed. Decreasing directional persistence in movement is generally considered to be a response to remain within a favorable habitat (*Buskey and Stoecker*, 1988; *Menden-Deuer and Grünbaum*, 2006; *Bianco et al.*, 2014). This is consistent with the fact that cyprids of *S. balanoides* have been observed to be concentrated near the surface, which has been shown to have a strong influence on the vertical distribution of settlement in the intertidal zone (*Grosberg*, 1982).

The persistence length influences predation risk, as the ratio of the persistence length of the prey to radius of prey detection of an ambush feeding predator ($e.g.$, chaetognath) determines the efficiency of the rate of search of the predator (*Visser and Kiørboe*, 2006; *Visser*, 2007; *Sorochan et al.*, 2017). I found that nauplii were generally characterized by higher persistence times and lower swimming speeds than cyprids, often resulting in similar persistence lengths among larval stages. Quantification of persistence length from trajectories characterized by swimming and sinking ($i.e.$, cyprids in my study) may lead to an overestimation of predation risk, as this swimming pattern has been shown to be far less

"risky" to predation ($i.e.$, encounter with predator) than looping patterns (*Bianco et al.*, 2014). I, therefore, suspect that the actual difference in predation risk between nauplii and cyprids is larger than that inferred from the persistence lengths measured in this study. This is consistent with my expectation that nauplii would exhibit a more "risky" behaviour than cyprids, as nauplii must search for food at the cost of increased exposure to predators.

Larval trajectories were approximately ballistic over a duration of at least 0.25 s as the minimum value of τ (0.29 s for cyprids at 12°C) was $>$ 0.25 s. The convergence of l/L to that expected from diffusive movement at small τ/t indicates that the entire transition from ballistic to diffusive movement occurs over a period of $\leq$ 6 s. This information can be used in future studies on the swimming behaviour of $S.balanoides$ when deciding on the appropriate time interval to use between observations, and minimum duration over which the transition from ballistic to diffusive movement occurs.

3.5.3 Directional bias in larval motility

The correlated random walk model (Equation 3.2) used to estimate persistence time and length assumes isotropic movement. I have shown that this is not the case in this study, as the magnitude of each swimming metric was greater in the vertical (z) dimension than the horizontal (x) dimension in almost all instances. This finding is not surprising, given the potential effects of gravity and pressure on larval behaviour. Many planktonic crustaceans swim upward in response to an increase in hydrostatic pressure, and this behaviour is important to depth regulation in the water column (*Lincoln*, 1971; *Forward*, 1989). Changes in hydrostatic pressure have been shown to influence the phototaxis of nauplii of *S. balanoides* (*Rice*, 1964), and the combined effects of light and pressure are believed to play an important role in the depth regulation behaviour of larval barnacles (*Walker et al.*, 1987).

Temperature has been shown to influence the vertical displacement of the blastula stage of sea urchins (*McDonald*, 2004) and the vertical distribution of larval marine benthic invertebrates (*Ouellet and Allard*, 2006; *Daigle and Metaxas*, 2011, 2012). Larval crabs and shrimp actively seek preferred temperatures by swimming downward or upward (*Forward*, 1990; *Ouellet and Allard*, 2006). With respect to N6, the interaction between directional persistence and temperature indicates that paths became increasingly ballistic in the vertical dimension as temperature increased. This behaviour is not consistent with "temperature seeking" because no correlation between NDGR_z and temperature

was observed. In contrast, the negative correlation between $NGDR_z$ and temperature is consistent with cyprids seeking warmer surface waters by net upward swimming at cool temperatures. However, a true test of the effect of temperature on larval swimming orientation requires temperature variation in space (*Walker et al.*, 1987), which did not occur in my study.

3.5.4 Conclusions

Larval swimming behaviour is an important source of variability in larval vertical distribution, transport, and recruitment dynamics. Data on motility traits are critical to the parameterization of larval movement in biophysical models that predict larval dispersal or population connectivity (*Fiksen et al.*, 2007; *Metaxas and Saunders*, 2009). In addition, motility data can provide insight into ecological consequences of the evolution of different life history strategies ($e.g.$, planktotrophy and lecithotrophy).

I have shown that temperature can influence the swimming speed and directional persistence of larval barnacles. I suggest that differences in the swimming behaviour among feeding and non-feeding larvae are at least in part driven by variability in the selective pressure to find food; however, in the case of larval barnacles, there are other factors to consider. For example, cyprids also use their motility to regulate their depth in the water column, which can influence horizontal transport (*Bousfield*, 1955; *Shanks and Wright*, 1987) and the vertical distribution of settled larvae on the shore (*Grosberg*, 1982).

The correlated random walk (CRW) model that I used assumes isotropic movement. My results indicated bias in swimming speed and directional persistence in the vertical dimension. Consequently, the swimming behaviour of larval barnacles in this study caused anisotropic spreading of individuals. In addition, the ability to apply CRW to actual swimming trajectories is limited because paths are assumed to be random, and therefore not organized in repetitive or oscillatory structure, which is clearly an oversimplification (*Bianco et al.*, 2014). I therefore caution the use of data from this study on directional persistence in the xz plane in models for the prediction of encounter rates or larval distributions. Despite the limitations of the CRW framework, I encourage the use of idealized models for the development of new hypotheses on the biology and ecology of larval marine benthic invertebrates.

CHAPTER 4

LOW PREDATION RATES ON THE LARVAE OF THREE SPECIES OF BARNACLES BY THE CTENOPHORE *Pleurobrachia pileus*

4.1 Abstract

Predation is considered a major source of mortality during the planktonic larval phase of most species of marine benthic invertebrates; however, direct estimates of predation are scarce. I estimated predation rates (d^{-1}) on nauplii of 3 species of barnacles (*Balanus balanus*, *Balanus crenatus*, *Semibalanus balanoides*) by the ctenophore *Pleurobrachia pileus* in the Northwest Arm, Halifax, in winter and early spring 2014. Ingestion rates (prey d^{-1}) were predicted from the number and digestion time of barnacle nauplii in the pharynx of *P. pileus*. Predation rates were estimated by multiplying the ingestion rate by the ratio of the predator to prey concentration. The digestion time (mean $\pm$ SE) of barnacle nauplii was significantly longer at 2°C (7.1 $\pm$ 0.4 h, n = 5 to 8.6 $\pm$ 0.3 h, n = 9) than at 6°C (4.9 $\pm$ 0.4, n = 6 to 6.6 $\pm$ 0.3 h, n = 8), in 3 laboratory experiments. The

Sorochan, K. A., and Metaxas, A. 2015. Low predation rates on the larvae of three species of barnacles by the ctenophore *Pleurobrachia pileus*. Marine Ecology Progress Series. 541: 105-122.

My coauthor Dr. Anna Metaxas supervised the study design and analysis, and edited the manuscript.

digestion time of cyprid larvae could not be reliably estimated because they were egested alive as freely swimming individuals or trapped within a prey bolus. Nauplii of *B. crenatus* were positively "selected for" by *P. pileus*, and estimates of predation rate were generally highest for this species. The predation rates of each species were frequently < 0.005 d^{-1}, indicating that predation by *P. pileus* was negligible. Concentrations of *P. pileus* were within the normal range for this area (on the order of 0.1 ind. m^{-3}) and probably would need to be sustained at anomalously high levels (1 to 10 ind. m^{-3}) to have an ecologically significant impact on populations of larval barnacles.

4.2 Introduction

Populations of most species of marine benthic invertebrates are seeded by the settlement of planktonic larvae. The spatial and temporal variability in the abundance of larvae and recruits is highly sensitive to variation in the magnitude of the mortality rate (*Underwood and Fairweather*, 1989; *Cowen et al.*, 2000). Reliable estimates of larval mortality are, therefore, critical to the accuracy of predictions of larval dispersal and population connectivity from biophysical models (*Metaxas and Saunders*, 2009). The disparity between the number of eggs produced and the abundance of adults within benthic populations indicates that the magnitude of mortality that occurs during early life stages must be enormous (*Thorson*, 1950); however, most estimates of larval mortality are uncertain, due to the difficulty of tracking larvae in nature (*Rumrill*, 1990). Vertical life table methods (*Aksnes and Ohman*, 1996) have recently been used to estimate stage-specific mortality rates of larval crustaceans (*Tapia and Pineda*, 2007; *White et al.*, 2014). This approach is promising, but is limited in its applicability because the model is dependent on the availability of data on durations of discrete larval stages, sensitive to cohort structure among larval stages, and dependent on several assumptions that require careful consideration (*Aksnes and Ohman*, 1996; *Gentleman et al.*, 2012).

Larval mortality may be caused by predation, starvation, disease, developmental abnormalities, physiological stress, and transport away from suitable habitat (*Thorson*, 1950; *Rumrill*, 1990). *Thorson* (1950)'s suggestion that predation is a major source of larval mortality has been supported by the high diversity of larval predators, presence of larval traits that defend against predation, and susceptibility of larvae to ingestion in the laboratory (see reviews by *Young and Chia*, 1987, *Rumrill*, 1990, and *Morgan*, 1995).

Few attempts have been made to measure larval predation directly. *Olson and McPherson* (1987) tracked ascidian larvae visually and found extremely high predation rates (0.41 s^{-1}) from ingestion by fish. *Allen and McAlister* (2007) tethered crab megalopae to moorings and also found high predation rates ranging from 0.62 d^{-1} in the water column during the day to 25.03 d^{-1} near the benthos at night. Lastly, *Johnson and Shanks* (2003) measured larval predation in mesocosms containing natural plankton assemblages and found low larval predation rates ranging from 0 to 0.07 d^{-1}. The variability in predation estimates among these studies highlights the need for further research on larval predation (*Vaughn and Allen*, 2010).

The magnitude of predation is a function of the predator community composition and the functional response of each predator (*Bailey and Houde*, 1989). Therefore, estimates of larval ingestion rates by predators that are abundant and readily feed on larvae are needed to assess the potential effect of predation on larval populations (*Vaughn and Allen*, 2010). The quantification of predation rates from specific predators requires the use of an ingestion rate model coupled with estimates of the abundance of the predator and its prey. This method has been used to study plankton grazing (*Båmstedt et al.*, 2000) and occasionally predation on larval fish (*Purcell*, 1981, 1989; *Jaspers et al.*, 2011; *Purcell et al.*, 2014). Reports of predation rates by specific predators on larvae of marine benthic invertebrates are rare (*Kuipers et al.*, 1990; *Hansson et al.*, 2005; *Hansson and Kiørboe*, 2006) and have not been presented in the context of their importance in larval ecology.

I evaluated predation rates of the nauplii of 3 species of barnacles from ingestion by the ctenophore *Pleurobrachia pileus* using a model that derives ingestion rate from the pharynx content of *P. pileus* and the digestion time of its prey (*Bajkov*, 1935). This approach is restricted to predators that consume their prey whole ($i.e.$, gelatinous zooplankton and fish), but does not require laboratory-derived estimation of ingestion rates, which are known to vary with turbulence (*Saiz and Kiørboe*, 1995), temperature (*Uye and Kayano*, 1994), the presence of other plankton (*Johnson and Shanks*, 1997), and container size (*Gibbons and Painting*, 1992).

In the Northwest Atlantic, the peak abundance of barnacle nauplii occurs in late winter and early spring (*Paranjape and Conover*, 1973; *Townsend*, 1984). Larval barnacles progress through 6 naupliar stages and a cyprid stage over a larval duration of several weeks (*Walker et al.*, 1987). *P. pileus* is commonly encountered in the zooplankton

communities of the Northwest Atlantic during the spring and summer (*Bigelow*, 1926). At this time, *P. pileus* may reach maximum concentrations on the order of 1 to 10 ind. m^{-3} off the coast of Nova Scotia (*Milne and Corey*, 1986).

The magnitude of predation by *P. pileus* on zooplankton depends on the encounter rate and susceptibility of prey to ingestion after capture (*Greene et al.*, 1986). *Frank* (1986) and *Båmstedt* (1998) estimated that *P. pileus* reduced crustacean zooplankton biomass by 8 to 9% d^{-1} when present at concentrations of ≤ 1 ind. m^{-3}. On the other hand, *Kuipers et al.* (1990) found that *P. pileus* reduced copepod densities at a rate on the order of 0.1 to 1% d^{-1} when present at concentrations on the order of 1 to 10 ind. m^{-3}. Larval barnacles are a component of the natural diet of *Pleurobrachia* spp. (*Fraser*, 1970; *Rowe*, 1971; *Hirota*, 1974; *Anderson*, 1974; *Frank*, 1986; *Larson*, 1987; *Kuipers et al.*, 1990; *Båmstedt*, 1998). *Kuipers et al.* (1990) estimated that the maximum predation rate of larval barnacles by predation from *P. pileus* was $\approx 2\%$ d^{-1}. However, these estimates may not be reliable as *Kuipers et al.* (1990) used copepod digestion times to estimate the ingestion rate, and did not identify larval barnacles to species.

In this study, I improved on previous estimates of predation rates on larval barnacles by *P. pileus* ($i.e.$, *Kuipers et al.*, 1990) by quantifying species-specific predation rates of barnacle nauplii, evaluating the digestion time of larval barnacles in the pharynx of *P. pileus*, assessing the validity of the assumptions associated with the estimation of predation rates, and quantifying the temporal variation in abundance of other potential pelagic predators over the duration of the study.

4.3 Methods

4.3.1 Sample collection

I obtained zooplankton samples in the Northwest Arm, Nova Scotia, Canada (Figure 4.1). The Northwest Arm is a small inlet (5 km long, 0.5 km wide) in Halifax, on the eastern coast of Nova Scotia, with a maximum depth of 18 m and flushing time of 2.7 d (*Gregory et al.*, 1993). At each of 2 sites, approximately 1.5 km apart (Site 1: 44°37'44" N, 63°35' 31"W, Site 2: 44°37'16" N, 63°34' 31"W, Figure 4.1), I conducted 2 successive oblique plankton tows (15 m to surface, 0.5 to 1 m s^{-1} tow speed) using a 0.75-m diameter plankton net (125-μm mesh size) with a General Oceanics flowmeter. On deck, I measured the polar diameter (length along oral-aboral axis) of individuals of *Pleurobrachia pileus* prior to

preserving the plankton sample in 95% ethanol.

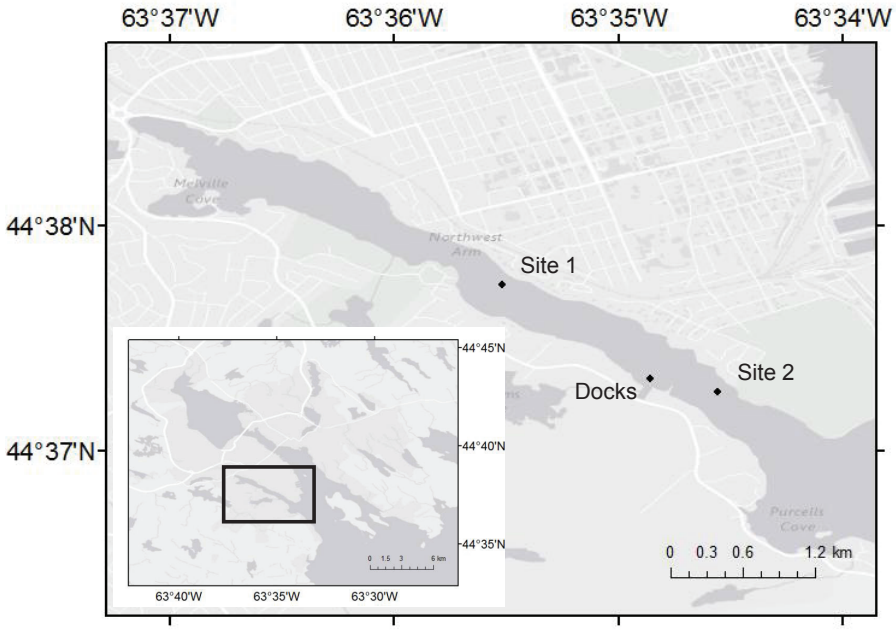

Figure 4.1: Halifax Harbour (inset) and Northwest Arm. Plankton tows were done at Sites 1 (44°37'44" N, 63°35' 31"W) and 2 (44°37'16" N, 63°34' 31"W). Individuals of *Pleurobrachia pileus* were collected for gut content analysis at docks. The Basemap was obtained from Esri ArcMap v. 10.3 software.

I did not use individuals of *P. pileus* obtained from plankton tows for pharynx content analysis because collection with plankton nets may cause unnatural feeding and egestion (*Båmstedt et al.*, 2000). Instead, on each sampling date, I collected 29 to 49 individuals of *P. pileus* from 1 m depth to the sea surface from an array of floating docks near the 2 sites where I conducted plankton tows (Figure 4.1). I collected *P. pileus* with a 10-cm diameter plastic container attached to a 1.5-m long stick. I measured the polar diameter of *P. pileus* before gently transferring each individual into a centrifuge tube containing 10% buffered formalin.

I collected samples in winter and spring 2014 and spring 2015. In all cases, I conducted plankton tows immediately before or after dipping. In 2014, I obtained samples weekly from 21 February to 30 April to determine the abundance of larval barnacles and *P. pileus* and the number of larval barnacles in the pharynx of *P. pileus* over most of the larval duration of the barnacles. On any one date, I collected plankton samples between 10:00 and 16:00 h and dipped ctenophores from docks near maximum ebb or flood tide between

11:30 and 15:30 h.

In 2015, I collected samples twice over a ≈ 24 h period, on 6 to 7 April and 15 to 16 April to quantify short-term variability in the abundance of *P. pileus* and larval barnacles and the pharynx content of *P. pileus*. On each pair of dates, I dipped ctenophores in the late afternoon or evening of Day 1 and in the early morning of Day 2 (Table C.1). I collected consecutive samples only twice because of poor weather in winter and apparent senescence of ctenophores in spring. I observed several individuals of *P. pileus* that were irregularly shaped and apparently in a state of disintegration during dipping on 15 to 16 April 2015. Collection of these individuals was avoided, and those that were collected were excluded from analysis.

In the laboratory, I split the plankton samples obtained from plankton tows with a Folsom splitter and enumerated larval barnacles and their potential predators. For n = 7, I counted all subsamples and determined that enumerating a minimum of 80 individuals of each species resulted in $< 10\%$ error. I identified larval barnacles to species and stage following *Crisp* (1962), *Lang* (1980), and *Branscomb and Vedder* (1982). Four species of balanid barnacles release larvae in the winter and spring months in the Northwest Atlantic including *Amphibalanus improvisus* (formerly *Balanus improvisus*), *Balanus balanus*, *Balanus crenatus*, and *Semibalanus balanoides* (*Bousfield*, 1954). Nauplii of *B. crenatus* and *A. improvisus* are morphologically similar (*Lang*, 1980), and no attempt was made to distinguish these species, which are collectively referred to hereafter as *B. crenatus*. I did not enumerate the first larval barnacle stage because this stage was not abundant in my samples and is difficult to identify to species. I identified barnacle cyprids as either *S. balanoides* or *Balanus* sp. I identified potential predators of larval barnacles following *Fahay* (1983) and *Johnson and Allen* (2012).

I excised the pharynx of each ctenophore collected from floating docks and enumerated the number of larval barnacles of each species. I grouped consecutive naupliar stages (Stages 2-3 and 4-5) because larvae partially digested or wrapped in mucus were difficult to identify to stage. All other prey items were identified as copepods, which I enumerated but did not identify further taxonomically. I only enumerated larval barnacles and copepods if they were intact and their exoskeleton had not been completely cleared of tissue (Figure 4.2A,B).

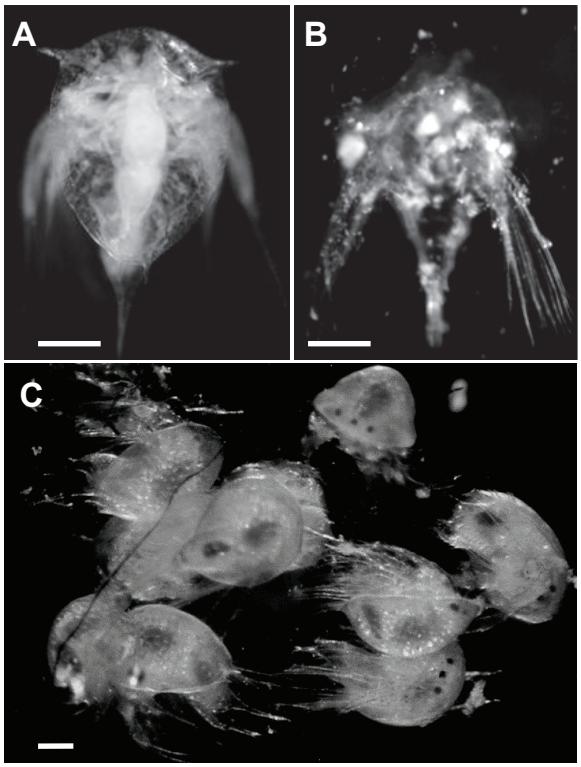

Figure 4.2: (A) Undigested nauplius of *Semibalanus balanoides*, (B) digested barnacle nauplius, and (C) bolus of several Stage 6 nauplii of *S. balanoides*. Scale bars = 200 μm.

4.3.2 Digestion experiments

I measured digestion time of barnacle nauplii in the pharynx of *P. pileus* at 2°C and 6°C in 3 experiments (Table 4.1). The temperature treatments reflected the range of temperatures measured from HOBO® pendant data loggers (accuracy ± 0.47°C; Onset Computer), deployed at depths of 1 and 10 m in the Northwest Arm over the field sampling period in 2014 (Figure C.1).

For each experiment, I collected ≈ 50 individuals of *P. pileus* from floating docks in the Northwest Arm, immediately transported them to the Dalhousie University Aquatron facility, and evenly allocated them in 2 cylindrical tanks (0.65 m diameter, 0.41 m height) filled with ≈ 100 l of continuously flowing sand filtered seawater. I then held the ctenophores for 24 to 72 h without food prior to feeding them larval barnacles (Table 4.1). In all cases, I acclimated the ctenophores at 2 or 6°C (± 0.5°C) for 24 h before feeding. In Expt 1, I acclimated the ctenophores immediately after collection, whereas in Expts 2 and 3, I acclimated the ctenophores after holding them at ambient temperature for 24 h or 48 h, respectively (Table 4.1).

After the acclimation period, I offered larval barnacles to *P. pileus* for 15 to 30 min. I transferred each ctenophore that had consumed at least 1 barnacle nauplius into a 200 ml beaker filled with 1-μm filtered seawater at 2 or 6°C (± 0.5°C). I placed the beaker in a temperature-controlled room maintained at the experimental temperatures. I monitored the temperature in each room throughout each experiment using a HOBO® pendant data logger (Table 4.1). I visually monitored larvae in the pharynx of each ctenophore at 30 min intervals, and recorded the time when each nauplius was completely cleared of tissue ($i.e.$, digested; Figure 4.2A,B). I defined the digestion time of each nauplius as the time elapsed between the time that *P. pileus* was transferred to the 200 ml beaker and the midpoint of the last 2 times the nauplius was checked. At the end of the experiment, I measured the polar diameter of each ctenophore.

Table 4.1: Details of methods used in digestion experiments. Temp: mean temperature measured during the experiment ± range of 0.2°C; N: number of ctenophores; Starvation period: sum of holding and acclimation periods; Meal size: number of larval barnacles fed to each ctenophore; Bb: *Balanus balanus*; Bc: *Balanus crenatus*; Sb: *Semibalanus balanoides*; lab: laboratory-reared.

Experiment, Treatment(°C)	**Date**	**Temp (°C)**	**N**	**Starvation period (h)**	**Mean ctenophore diameter ± SD (cm)**	**Prey type (species; stage)**	**Meal size (min, max)**
1, 2	30 Mar 2014	2.52	9	24	1.79 ± 0.37	Sb (lab); 3-4	1, 1
1, 6	30 Mar 2014	5.55	8	24	1.85 ± 0.20	Sb (lab); 34	1, 1
2, 2	12 Apr 2014	1.76	8	48	2.08 ± 0.22	Bb, Bc, Sb; 4-6	1, 9
2, 6	12 Apr 2014	6.17	8	48	1.99 ± 0.12	Bb, Bc, Sb; 4-6	1, 10
3, 2	13 Apr 2014	2.52	5	72	1.58 ± 0.31	Bb, Bc, Sb; 4-6	1, 2
3, 6	13 Apr 2014	5.76	6	72	1.86 ± 0.46	Bb, Bc, Sb; 4-6	2, 12
4, 6	12 Mar 2015	6	13	72	–	Sb (lab); 6	2, 29
5, 6	4 Apr 2015	6	34	36	–	Sb (lab); cyprid	1, 22

In Expt 1, I offered the ctenophores Stage 3-4 nauplii of *S. balanoides* reared in the laboratory. I induced larval release by feeding adults high concentrations of diatoms (*Thalassiosira weissflogii*), and cultured the larvae at a concentration of 1 larva ml^{-1} in 4 l glass jars containing 1-μm filtered seawater at 6°C, and 10^5 phytoplankton cells ml^{-1} (3 to 1 mixture of *T. weissflogii* to *Isochrysis* sp.). In Expts 2 and 3, I offered the ctenophores a mixture of 3 species of Stage 4-6 nauplii (Table 4.1) collected from horizontal plankton tows (0.75 m diameter plankton net with closed cod end) near the sea-surface in the Northwest Arm. Prior to the experiment, I kept these larvae under the same culture conditions as *S. balanoides* in Expt 1.

I attempted to conduct similar experiments with field-collected barnacle cyprids as prey, but the majority of ctenophores egested all cyprids prey within hours of feeding. This was unexpected, as only a single barnacle nauplius was egested in the nauplii digestion experiments described above. To further investigate larval digestion and egestion, I conducted 2 additional experiments using laboratory-reared sixth stage nauplii and cyprids of *S. balanoides* as prey (Expts 4 and 5, Table 4.1). For these experiments, I held each ctenophore in a 5.7 l PVC cylinder (radius = 10 cm, height = 18 cm) with a 120-μm Nitex mesh bottom immersed in continuously flowing sand-filtered sea water at 6°C while digesting their prey. I used this holding container to prevent stress-induced larval egestion that may have occurred in previous experiments, when the ctenophores were held in much smaller (200 ml) containers, and accommodate ctenophores digesting larvae over long time periods. I monitored temperatures throughout these experiments using a hand-held thermometer. I checked the pharynx content of the ctenophores, and removed egested prey from the holding containers at $\approx$ 15 min intervals to prevent re-ingestion of egested prey. I removed ctenophores that had egested all of their prey from their container and replaced them with newly fed ctenophores. Egested prey were either expelled alive individually or as part of a bolus composed of many prey items held together by mucus (Figure 4.2C).

4.3.3 Data analysis

4.3.3.1 Prey composition

For each sampling date, I compared the observed frequency of each species of barnacle nauplii in the pharynx of *P. pileus* (larvae pooled across ctenophores) with the expected frequency calculated from the proportion in the plankton (larvae pooled across sites) using χ^2 -tests. To determine whether each species was over- or under-represented in the pharynx,

I calculated a selectivity index, β, following *Chesson* (1978):

$$\beta_a = \frac{p_{gut_a}/p_{env_a}}{\sum_{i=1}^{n} p_{gut_i}/p_{env_i}} \tag{4.1}$$

where p_{gut} is the proportion of larvae in the pharynx and p_{env} is the proportion of larvae in the plankton. The subscript a represents the species of interest, in n species of prey. For $\beta_a < 0.5$, a lower proportion of prey type a was found in the pharynx than the plankton. For $\beta_a > 0.5$, a higher proportion of prey type a was found in the pharynx than the plankton. Lastly, for $\beta_a = 0.5$, prey type a was found in equal proportions in the pharynx and plankton. I did not include cyprid larvae in this analysis, as they were not identified to species.

4.3.3.2 Size and pharynx contents of *P. pileus*

A mismatch between the polar diameters of individuals collected from plankton tows and those dipped from floating docks could bias projected feeding rates (see following subsection) if there is a relationship between ctenophore size and the number of larval barnacles in the pharynx. I explored the relationship between polar diameter and the total number of barnacle nauplii consumed for each survey using a generalized linear model with a negative binomial error structure and log-link function. I used a negative binomial error structure (rather than Poisson) because the ratio of variance to mean indicated the data were aggregated (variance to mean ratio > 1, in all cases). I tested the hypothesis that the mean polar diameter of individuals of *P. pileus* collected by dipping was greater than that collected by plankton tow using a 1-tailed Student's t-test. I did not include individuals of *P. pileus* with a polar diameter < 0.3 cm in the estimates of ctenophore abundance from the plankton samples because the polar diameter of ctenophores collected for pharynx content analysis was always > 0.5 cm.

4.3.3.3 Prey digestion time and barnacle predation rate

For Expts 1 to 3, I examined the effects of temperature (fixed factor, 2 levels) and experiment (random factor, 3 levels) on digestion time with a 2-way ANOVA using Type III SS due to unbalanced sample size (Table 4.1). I did not test for normality because the sample sizes were low ($5 \leq$ n ≤ 9); this was not a concern because ANOVA is robust to deviation in normality (*Underwood*, 1997). The Levenes test indicated that variances were not significantly heterogeneous (P = 0.97). I used the mean digestion time from Expts 1, 2, and 3 at 2°C (8.1 h) to estimate the average ingestion rate I (prey d^{-1}) of *P. pileus* on each

species of larval barnacle on each sampling date. This digestion time represents an over all average value from experiments that used different prey types, meal sizes (number of prey ingested), and acclimation/starvation periods (Table 4.1). I estimated the mean ingestion rate on each sampling date following *Bajkov* (1935):

$$I = \sum_{i=1}^{n} \frac{G_i}{Q}/n \tag{4.2}$$

where G_i is number of prey in the pharynx in the i^{th} ctenophore, Q is the digestion time (d), and n is the number of ctenophores examined for gut contents.

Bajkov (1935)'s model requires that the following assumptions are met: (1) the rate of change of G_i is in steady state ($i.e.$, ingestion rate equals digestion rate; *Bromley*, 1994) and (2) prey are digested linearly over the time after the first prey item is digested (*Bochdansky and Deibel*, 2001). I investigated the validity of these assumptions using data from digestion experiments. Assumption 1 is supported if there is no relationship between digestion time and meal size, in which case the digestion rate increases with meal size, and therefore with ingestion rate. I evaluated the relationship between the average digestion time and initial meal size for each ctenophore using simple linear regression. Assumption 2 is supported if there is a negative linear relationship between the number of undigested prey in the pharynx of *P. pileus* and the time after the first prey item is digested. I fitted a power model ($y = ax^c$) to this relationship and tested for non-linearity by examining the confidence interval of the exponent, c. Only relationships between undigested pharynx content and time with a minimum of 5 data points were evaluated (n = 8 ctenophores).

Ingestion rates can be potentially affected by prey egestion. Egestion of individual live prey will result in an overestimate of ingestion rates because it is assumed that all prey in the pharynx are killed and digested. Undigested prey were frequently egested as a bolus, and probably would die if unable to detach from one another. This would result in an underestimate of effective ingestion rates (ingestion that results in prey mortality) because the egestion time is inherently shorter than the digestion time. To explore the extent to which ctenophore egestion may affect estimates of ingestion rate, I computed the median egestion time (pooled among ctenophores) from Expts 4 and 5 (Table 4.1), as well as the frequency of ctenophores that egested prey as a bolus.

For each sampling date, I estimated the mean predation rate, M (d^{-1}), for nauplii of each barnacle species from predation by *P. pileus* as:

$$M = \frac{IC_{pred}}{C_{prey}} \tag{4.3}$$

where C_{pred} and C_{prey} are the mean concentrations of *P. pileus* and barnacle nauplii (no. m^{-3}), respectively, averaged across the 2 sampling sites (Figure 4.1). The standard deviation of M was calculated by propagating the error of I (from Q), C_{pred}, and C_{prey} *Hughes and Hase* (2010). The standard deviation associated with Q was calculated from the pooled variance among experiments (*Zar*, 1984). By not propagating error in G, I assume that the mean number of barnacle nauplii eaten per ctenophore is an accurate representation of predation within the ctenophore population. Cyprid larvae were not included in this analysis because their digestion time is unclear. All analyses were carried out using R v.3.1.1.

4.4 Results

4.4.1 Zooplankton concentrations and pharynx contents of *Pleurobrachia pileus*

Balanus balanus was the most abundant species of larval barnacle throughout the sampling period in 2014, peaking in concentration on 7 March (Figure 4.3A). Concentrations of larval *Semibalanus balanoides* and *B. crenatus* peaked on 17 March and 2 April 2014, respectively (Figure 4.3A). Progression through the developmental stages was exhibited by larvae of all barnacle species from 21 February to 2 April 2014, and was characterized by a decline in abundance of the second naupliar stage and an increase in abundance of successive stages (Figure 4.3). The proportion of Stage 6 nauplii of *S. balanoides* decreased and earlier naupliar stages of this species became relatively more abundant over the last 4 sampling dates (Figure 4.3B). Cyprid larvae first appeared on 2 April 2014; cyprids of *S. balanoides* and *Balanus sp.* peaked in abundance on 9 and 17 April 2014, respectively (Figure C.2).

The abundance of *P. pileus* fluctuated over the sampling period in 2014, but gradually decreased between 21 February and 30 April (Figure 4.4A); the polar diameter of ctenophores gradually increased over the same period (Figure 4.4B,C). A wide range of other (potential) predators were collected from the plankton tows (Table C.2), but only a few were consistently abundant throughout the sampling period (Figure 4.5).

In 2014, the number of prey items in the pharynx of *P. pileus* was composed of at least 70% larval barnacles, except on 21 February and 23 April (Figure 4.6). Barnacle cyprids appeared in the diet of ctenophores from 2 to 30 April 2014, but were not as abundant in the diet as were nauplii (except on 23 April 2014). The pharynx of any ctenophore was never completely full in this study. The mean and maximum number of nauplii retrieved from the pharynx of *P. pileus* varied from 0.66 to 10.0 nauplii ctenophore^{-1} and 3 to 70 nauplii ctenophore^{-1}, respectively (Figure 4.7A). The mean and maximum number of cyprids retrieved from the pharynx of *P. pileus* varied from 0.1 to 2 cyprids ctenophore^{-1} and 2 to 14 cyprids ctenophore^{-1}, respectively, from 2 to 30 April 2014 (Figure C.2B). Nauplii of *B. balanus* dominated the pharynx contents from 2 to 25 March 2014, but their frequency slowly declined thereafter (Figure 4.7B). In contrast, nauplii of *B. crenatus* were rarely found in the pharynx from 2 to 25 March 2014, but became the dominant prey item by 30 April 2014 (Figure 4.7B). The majority of cyprid larvae in the diet of *P. pileus* were *Balanus* sp. from 17 to 30 April (Figure C.2C).

Prey selectivity (β index; *Chesson*, 1978) was consistent across sampling dates, and χ^2-tests indicated that the null hypothesis of no preference was rejected ($P < 0.05$) in all cases except for *B. balanus* on 2 April (Table C.3). I therefore calculated these statistics for data pooled across sampling dates. *P. pileus* selected against *B. balanus* (β_{pooled} = 0.11; χ^2_{pooled} = 179) and *S. balanoides* (β_{pooled} = 0.06; χ^2_{pooled} = 150), but selected for *B. crenatus* (β_{pooled} = 0.83; χ^2_{pooled} = 2260). On 4 of the 10 sampling dates in 2014, the number of prey in the pharynx was significantly positively related to the polar diameter of *P. pileus* (Figure C.3). On 6 of the 10 sampling dates, the polar diameter of *P. pileus*, collected by dipping from floating docks, was significantly greater than individuals collected from plankton tows (Table 4.2).

In 2015, *S. balanoides* was the most abundant species of larval barnacle in April (Figure C.4A). The variability between samples collected on consecutive sampling dates was low for each species, except for *S. balanoides* on 6 to 7 April (Figure C.4A). The mean abundance of *P. pileus* was < 0.1 ind. m^{-3} and was consistent between sampling dates (Figure C.4B). The mean number of nauplii per ctenophore ranged from 0.05 nauplii on 16 April to 0.7 nauplii on 7 April (Table C.1).

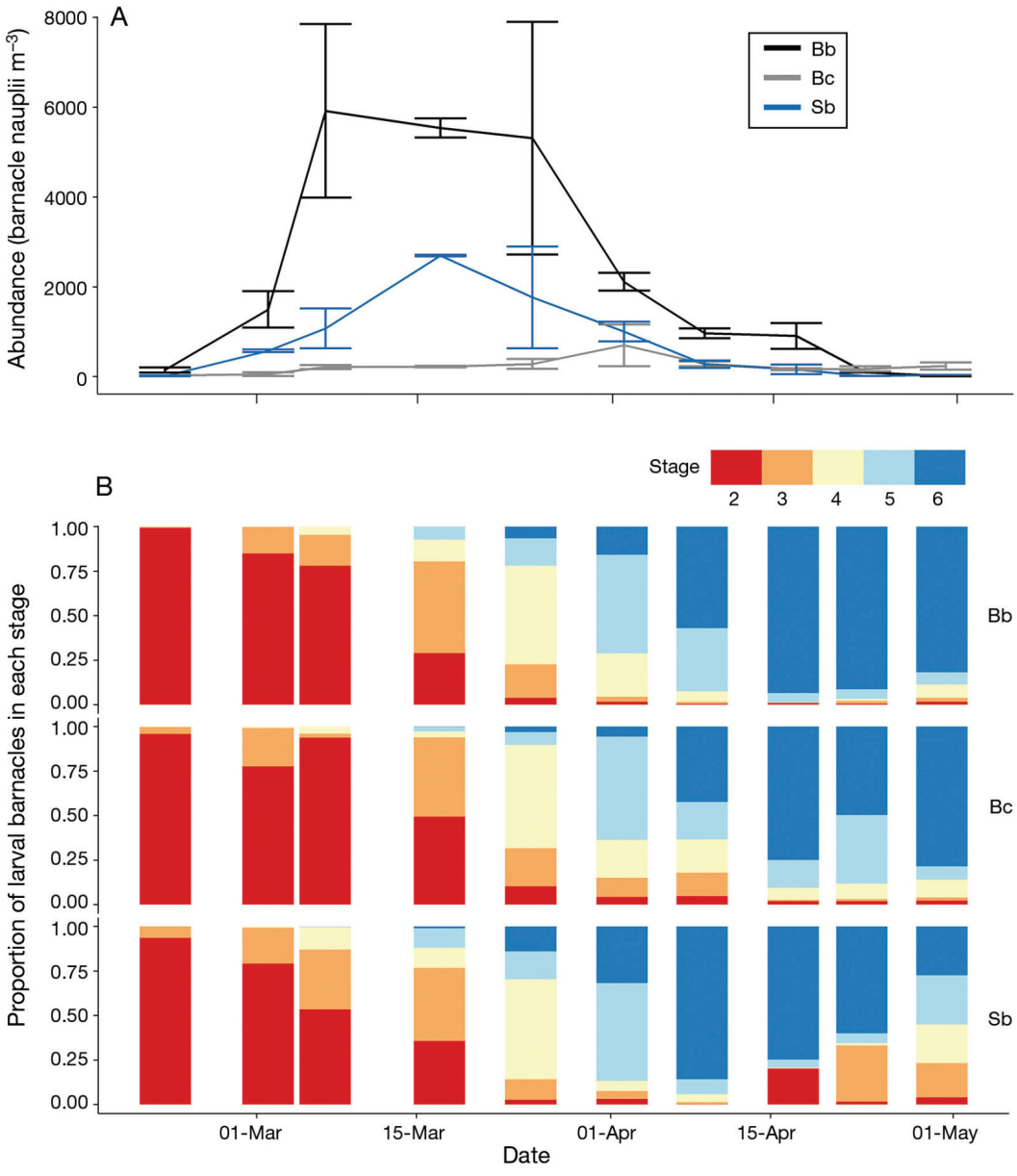

Figure 4.3: Time series of (A) mean ($\pm$1 SE; n = 2 sites) concentrations of nauplii of *Balanus balanus* (Bb), *Balanus crenatus* (Bc), and *Semibalanoides balanoides* (Sb) and (B) proportions of each naupliar stage pooled across sites.

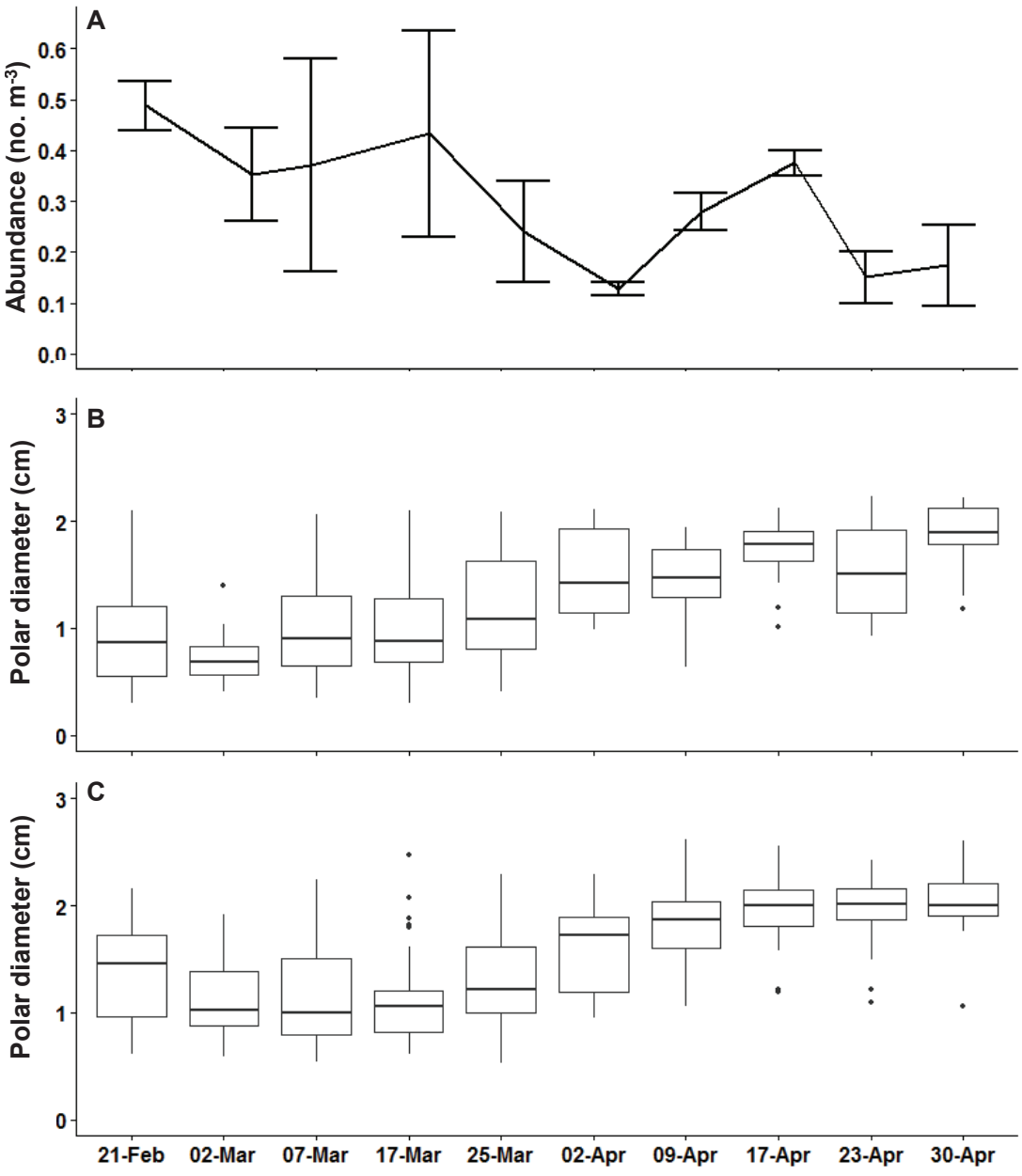

Figure 4.4: (A) Time series of mean ($\pm$ 1 SE; n = 2 sites) concentrations of ctenophores. (B,C) Box plots (median $\pm$ interquartile range [IQR]; whiskers 1.5 IQR) of polar diameters of *Pleurobrachia pileus* collected by (B) plankton tow and (C) dip net.

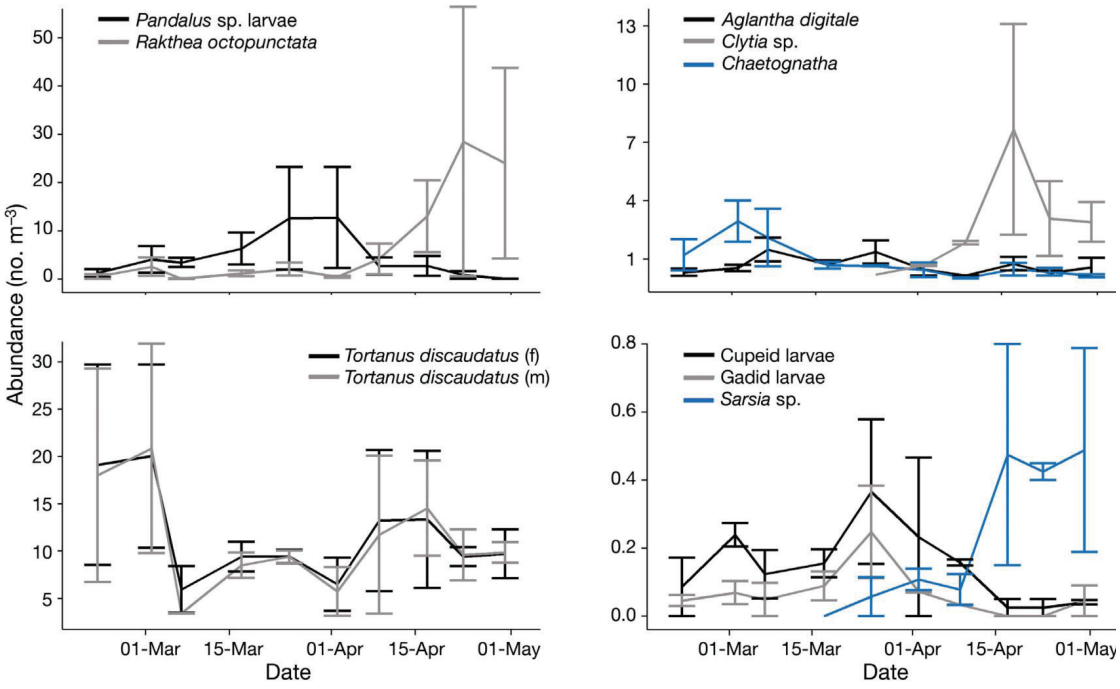

Figure 4.5: Time series of mean ($\pm$ 1 SE; n = 2 sites) concentrations of some potential predators of barnacle nauplii. Note the different scales on y-axes. f: female; m: male.

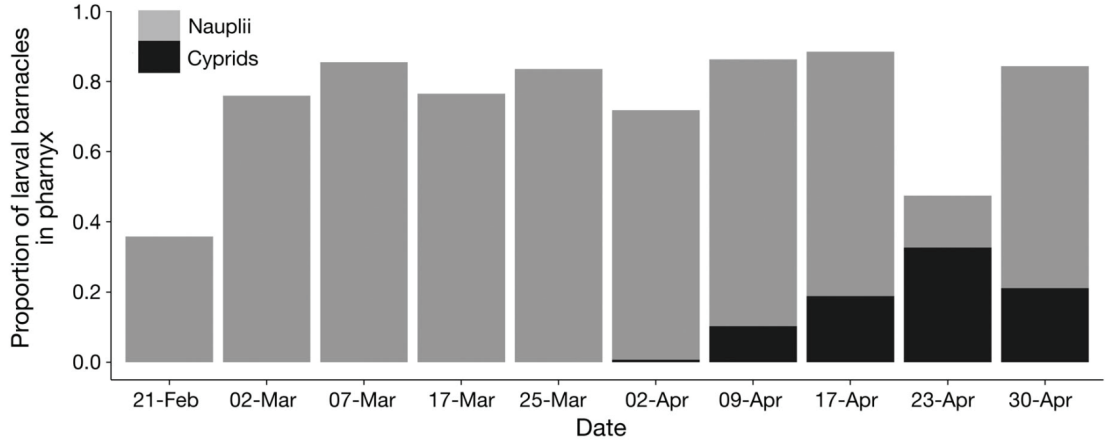

Figure 4.6: The proportion of larval barnacles in the pharynx of *Pleurobrachia pileus* (pooled across ctenophores). Prey items other than larval barnacles consisted of unidentified copepods.

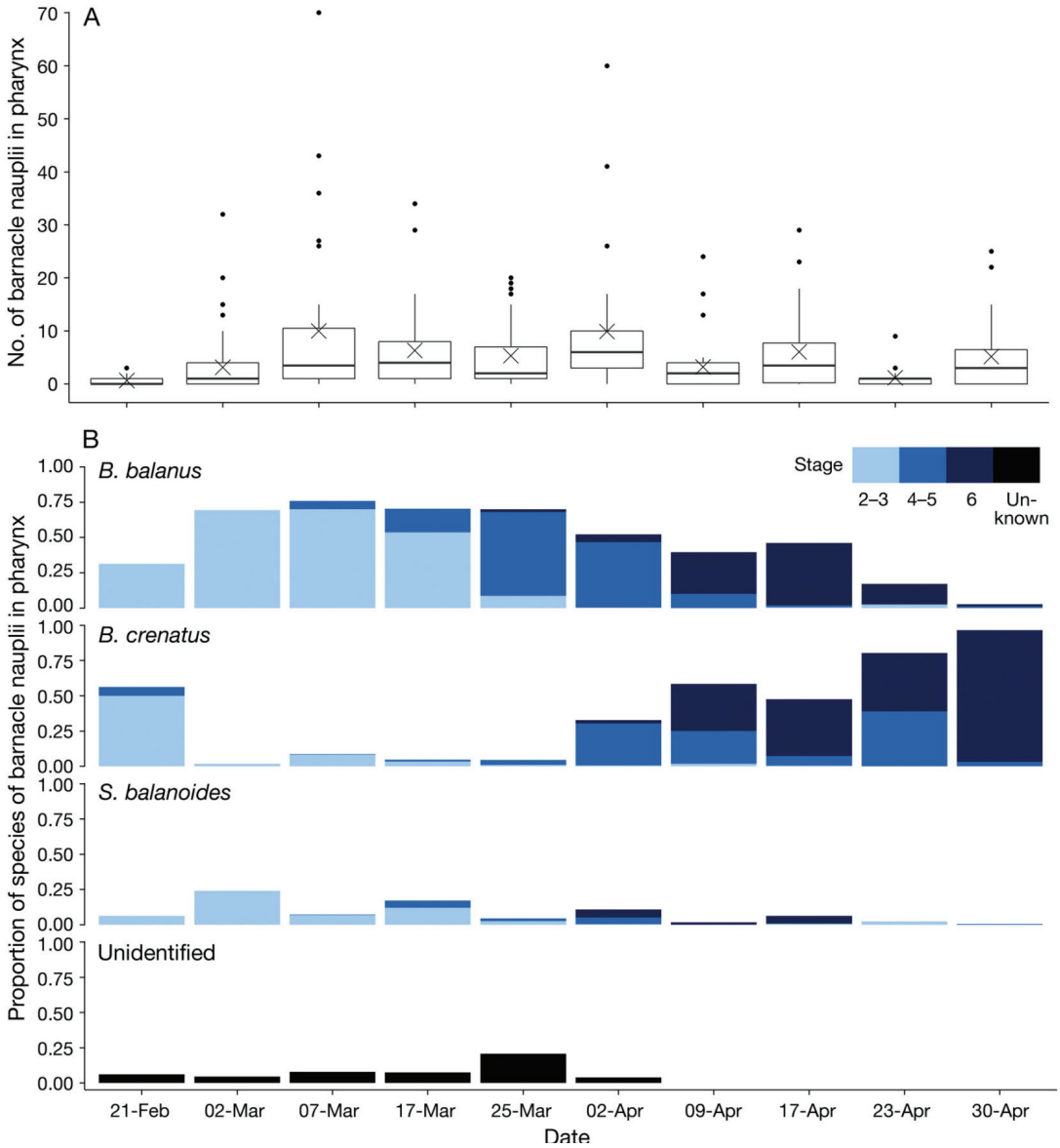

Figure 4.7: Description of barnacle nauplii recovered from the pharynx of *Pleurobrachia pileus*. (A) Box plots (median ± interquartile range [IQR]; whiskers 1.5 IQR; X denotes mean) of the number of barnacle nauplii (species combined) per ctenophore. (B) The proportion of barnacle nauplii (pooled across ctenophores) catagorized as *Balanus balanus*, *Balanus crenatus*, *Semibalanoides balanoides*, and unidentified. Stacked bars represent naupliar stages. Stages not specified for "unidentified" category.

Table 4.2: Results from analyses used to determine if a bias in ctenophore size affected the calculation of predation rates; t-tests were used to compare the polar diameter among ctenophores collected by dip and plankton tow methods. Generalized linear models (GLM; negative binomial error structure, log link) were used to determine the relationship between ctenophore size and the number of barnacle nauplii recovered from the pharynx. Significant differences (α = 0.05) are in bold.

Date	t-test			GLM			
	t-statistic	df	P	z-statistic	Residual df	Residual deviance	P
21 Feb 2014	3.57	60	< **0.001**	-2.55	26	27.36	**0.017**
2 Mar 2014	5.10	68	< **0.001**	1.03	48	49.68	0.304
7 Mar 2014	1.45	59	0.077	-0.42	28	33.95	0.677
17 Mar 2014	1.33	70	0.093	2.93	31	37.01	**0.003**
25 Mar 2014	1.07	59	0.145	2.42	35	40.90	**0.015**
2 Apr 2014	0.39	34	0.351	2.57	28	33.33	**0.010**
9 Apr 2014	3.83	47	< **0.001**	-0.26	30	34.77	0.799
17 Apr 2014	2.54	47	**0.007**	-0.01	32	38.55	0.989
23 Apr 2014	2.98	38	**0.002**	-1.46	32	34.16	0.144
30 Apr 2014	1.81	41	**0.040**	-0.61	31	35.79	0.545

4.4.2 Digestion time and predation rate of larval barnacles

Mean digestion times from Expts 1 to 3 were significantly longer at 2°C than at 6°C and varied significantly among experiments (Figure 4.8, Table 4.3). At 2°C, mean digestion times ($\pm$SE) ranged between 7.1 $\pm$ 0.4 h (n = 5) and 8.6 $\pm$ 0.3 h (n = 9). At 6°C, mean digestion times ranged between 4.9 $\pm$ 0.4 h (n = 6) and 6.6 $\pm$ 0.3 h (n = 8). The mean digestion time ($\pm$SE) from Expt 4 (at 6°C) was 4.0 $\pm$ 0.2 h.

Table 4.3: Results of 2-way ANOVA (Type III SS) examining the effects of experiment (random factor) and temperature (fixed factor, 2 levels: 2°C, 6°C) on digestion time of barnacle nauplii in the pharynx of *Pleurobrachia pileus*. Significant differences (α = 0.05) are indicated in bold.

Source	SS	df	F-statistic	P
Experiment	24.3	2	14.3	< **0.001**
Temperature	57.9	1	48.8	**0.020**
Experiment x Temperature	2.37	2	1.40	0.244
Residual	32.1	40	–	–

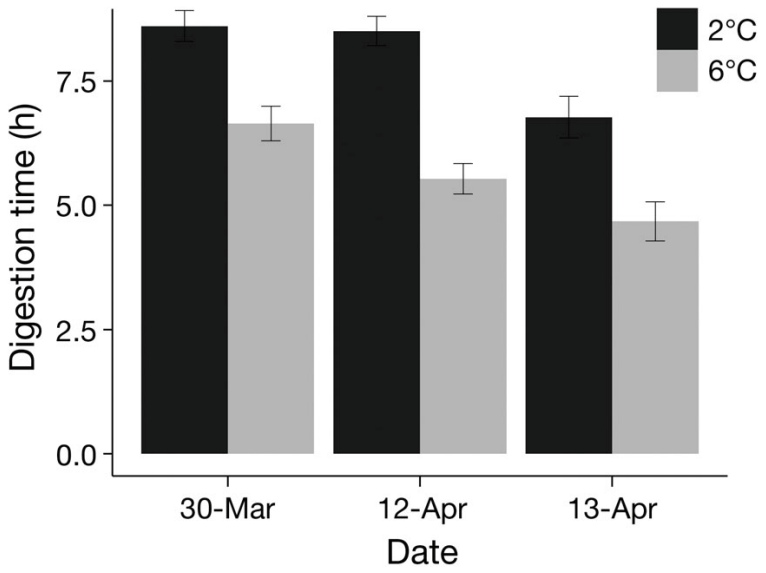

Figure 4.8: Mean (± 1 SE) digestion time of barnacle nauplii in the pharynx of *Pleurobrachia pileus* from Expts 1 to 3. See Table 4.1 for sample size and other methodological details on each experiment.

No significant relationship was detected between meal size and the average digestion time of *P. pileus* (Table C.4). Also, 5 of the 8 relationships between the number of undigested nauplii in the phanyx of *P. pileus* and time were determined to be non-linear (Figure 4.9).

Based on 4 observations in experiments carried out in 2014, the observed minimum cyprid digestion times were 23 and 17 h at 3 and 7°C, respectively. In Expts 4 and 5, 77% of ctenophores egested at least 1 nauplius and all ctenophores egested cyprids. Also, a prey bolus of at least 2 larvae was formed by 60% of ctenophores that egested nauplii, and 42% of ctenophores that egested cyprids. Median times to egestion of nauplii and cyprids were 0.5 and 0.3 h, respectively (Figure 4.10).

The predation rates that I estimated were generally greater for *B. crenatus* than for *B. balanus* and *S. balanoides* throughout the sampling period (Figure 4.11). In general, predation rates of *B. balanus* and *B. crenatus* declined from 21 February to 25 March 2014, then increased from 2 to 30 April 2014.

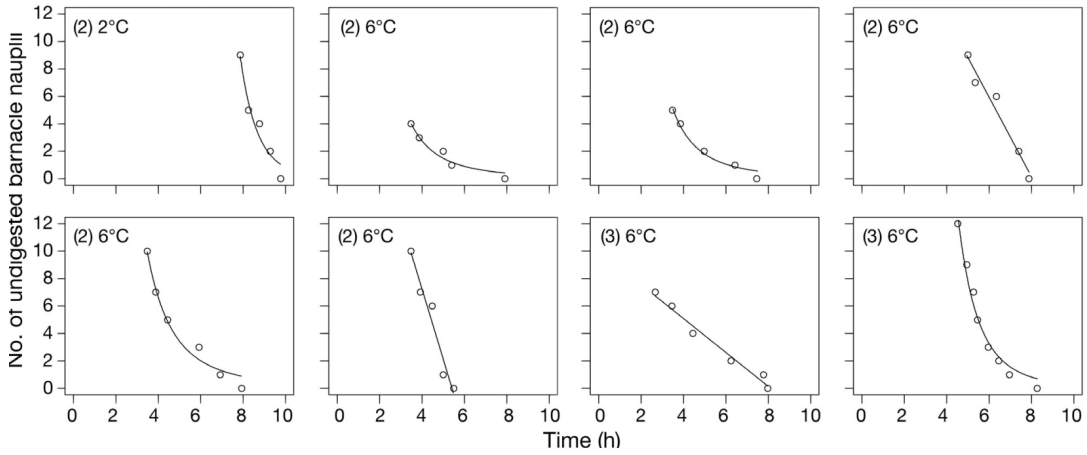

Figure 4.9: Relationships between the number of undigested nauplii in the pharynx of a ctenophore and time, fitted with linear or power ($y = ax^c$) models. Non-linear relationships indicate a lower confidence limit of parameter c < 1. The experiment number (in parentheses) and temperature treatment (see Table 4.1) are presented in each panel.

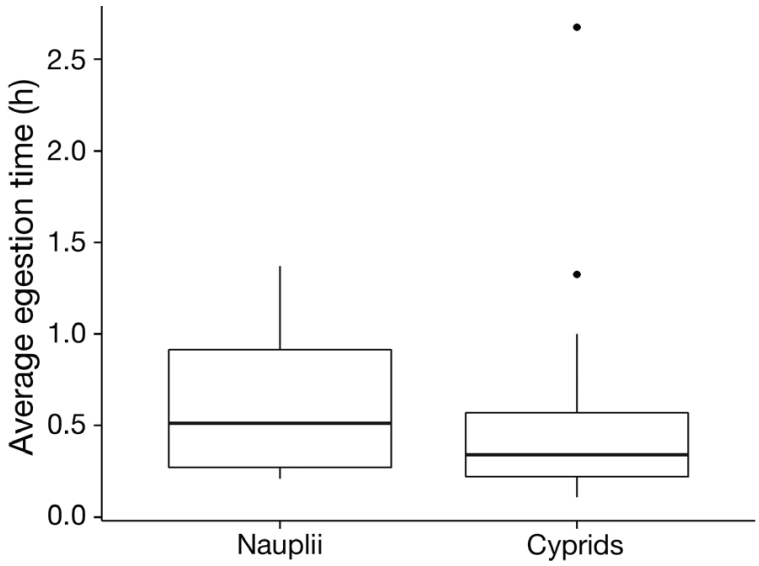

Figure 4.10: Box plots (median $\pm$ interquartile range [IQR]; whiskers 1.5 IQR) of average egestion times for each ctenophore.

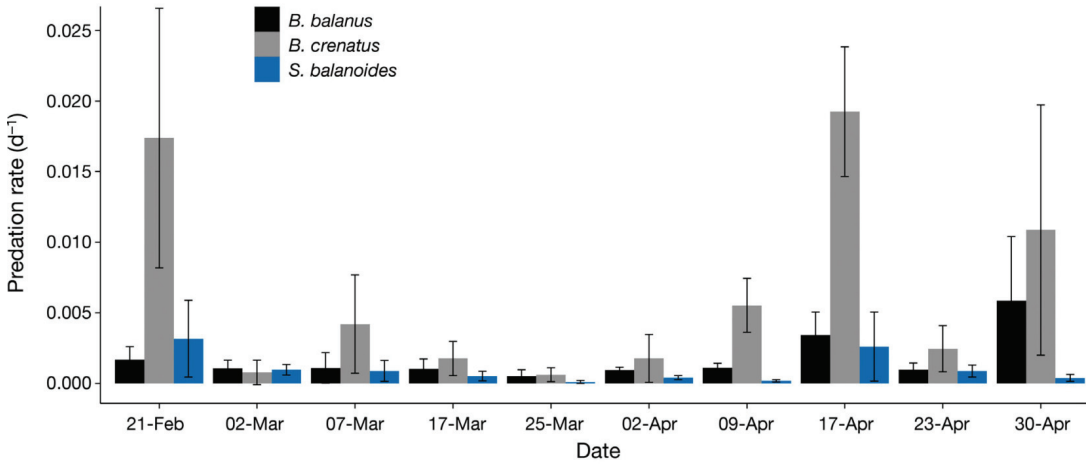

Figure 4.11: Mean instantaneous mortality rate (± 1 SD) of larval *Balanus balanus*, *Balanus crenatus*, and *Semibalanoides balanoides* from ingestion by *Pleurobrachia pileus* over the sampling duration. SD propagated from prey concentration (n = 2) and the pooled SD among digestion time experiments (each with different n, see Table 4.1)

4.5 Discussion

4.5.1 Phenology of prey and predators

The abundance and stage progression of *Balanus balanus* and *Semibalanus balanoides* indicated that hatching occurred primarily in early and mid-March, respectively. This is consistent with previous observations of hatching of *B. balanus* and *S. balanoides* occurring primarily in late winter or spring in the Northwest Atlantic (*Bousfield*, 1954; *Lang and Ackenhusen-Johns*, 1981). In this study, larval *Balanus crenatus* were present in winter and early spring, as previously reported by *Lang and Ackenhusen-Johns* (1981), although the primary hatching period of this species was reported to occur later in the spring and summer by *Bousfield* (1954, 1955). Variability in the abundance and size of *Pleurobrachia pileus* over the study period is consistent with the dynamics of this species in the region (*Milne and Corey*, 1986; *Matsakis and Conover*, 1991).

Other carnivorous zooplankton that were present and are known to feed on larval barnacles *in situ* include larval pandalid shrimp (*Stickney and Perkins*, 1981), larval gadid and clupeid fish (*Marshall et al.*, 1937; *Bainbridge and McKay*, 1968), chaetognaths

(*Alvarez-Cadena*, 1993), and hydrozoan jellyfish ($e.g.$, *Aglantha digitale*, *Clytia* sp., *Rakthea octopunktata*, *Sarsia* sp.; *Purcell and Mills*, 1988). The copepod *Tortanus discaudatus* likely feeds on barnacle nauplii as this species ingests large copepods (*Ambler and Frost*, 1974; *Mullin*, 1979). A different species of *Tortanus* has been observed feeding on barnacle nauplii in the laboratory (*Uye and Kayano*, 1994).

Because the majority of larvae were released in early March, the temporal overlap of larval barnacles with cnidarian predators was minimal, as several hydrozoan medusae (*Clytia* sp., *R. octopunktata*, and *Sarsia* sp.) only co-occurred with late larval stages. Cnidarian medusae typically become abundant in late spring and summer in the study region (*Bigelow*, 1926; *Matsakis and Conover*, 1991). However, multiple predators were present during most of the larval duration of each barnacle species, including *P. pileus*, *T. discaudatus*, chaetognaths, larval fish, and larval shrimp. Future studies on the impact of these predators on larval barnacle populations would be useful in assessing the overall importance of carnivorous zooplankton on larval barnacle mortality in the region.

4.5.2 Magnitude of predation

I estimated low predation rates on larvae of each species of barnacle from predation by *P. pileus* over the sampling period, frequently on the order of 0.001 d^{-1}. Over a 6 wk naupliar duration (*Bousfield*, 1954), this predation rate would reduce the larval population by only $\approx 5\%$. My estimates of the predation rate were low mainly because the abundance of larvae of each barnacle species was frequently at least 3 orders of magnitude more abundant than that of *P. pileus*. The total concentration of early stage barnacle nauplii was frequently on the order of 1 to 10 larvae l^{-1}, which is within the range of concentrations reported in the Northwest Atlantic (*Bousfield*, 1955; *Townsend*, 1984). The concentration of *P. pileus* in this study was also similar to those observed in previous studies in this region (*Frank*, 1986; *Milne and Corey*, 1986; *Matsakis and Conover*, 1991). Therefore, my results appear to be representative of normal conditions, and I conclude that it would require an anomalously high abundance of *P. pileus* (1 to 10 ind. m^{-3}) sustained over long periods to substantially reduce populations of barnacle nauplii in the Northwest Arm.

Predation rates on *B. crenatus* were generally the highest among barnacle species. This is consistent with *B. crenatus* being positively "selected" over the other barnacle species. This may have occurred because larval *B. crenatus* exhibited a higher degree of spatial overlap with *P. pileus*, were easier to capture and ingest, and were digested at a slower rate. Each

species of barnacle was consistently selected either for or against over the study duration, suggesting that changes in the abundance or stage composition of barnacle nauplii did not substantially change their selectivity to *P. pileus* relative to the other barnacle species on any one sampling date.

Although larval barnacles are frequently reported in the digestive tract of predators (*Marshall et al.*, 1937; *Bainbridge and McKay*, 1968; *Fraser*, 1970; *Stickney and Perkins*, 1981; *Purcell and Mills*, 1988; *Alvarez-Cadena*, 1993), estimates of predation rates are scarce. Available estimates are based on concentrations of larval barnacles not identified to species and on ingestion rates that were either extrapolated from laboratory incubations (*Hansson and Kiørboe*, 2006) or from digestion times estimated indirectly (*Kuipers et al.*, 1990; *Hansson et al.*, 2005). *Kuipers et al.* (1990) reported predation rates of larval barnacles (nauplii and cyprids) by *P. pileus*, but used the digestion time of copepods to evaluate predation rates. Using data provided in *Kuipers et al.* (1990) (their Table 1 and Fig. 9) and the barnacle nauplii digestion time provided by *Larson* (1987) (his Table 4) for *Pleurobrachia bachei* at 12 to 14°C, I estimated that predation rates of barnacle nauplii from *Kuipers et al.* (1990) were similar to those in this study, on the order 0.0001 to 0.001 d^{-1} and reached $\approx$ 0.01 d^{-1} on only one occasion. In contrast to this study, *Kuipers et al.* (1990) reported lower average numbers of larval barnacles in the pharynx ($\approx$ 0.01 to 1 larva ctenophore^{-1}) and higher concentrations of ctenophores (1 to 10 ctenophores m^{-3}). *Hansson and Kiørboe* (2006) also estimated low predation rates of barnacle nauplii from ingestion by *Sarsia* sp. (often < 0.001 d^{-1}). *Hansson et al.* (2005) reported average predation rates of larval barnacles from ingestion by *Aurelia aurita* in Limfjorden, Denmark, ranging from 0.01 d^{-1} in May to 0.10 d^{-1} in July. The authors suggested that *A. aurita* was capable of controlling larval barnacle populations.

The high level of temporal variability in predation rates of *B. crenatus* in this study and of barnacle nauplii in *Hansson et al.* (2005) underscores the importance of sampling at different times during the larval period. Variability in predation rate is caused by factors that influence (1) the ingestion rate and (2) the abundance of predator and prey populations. As larvae develop, their morphology, behaviour, and swimming and sensory abilities change (*Chia et al.*, 1984; *Kingsford et al.*, 2002). These factors likely influence their vulnerability to ingestion (*Pennington et al.*, 1986). For example, *Greene et al.* (1986) attributed stage-specific variation in the clearance rate of copepods by *P. bachei* to

differences in swimming speed and post-encounter escape abilities of the prey. Ontogenetic variation in vertical distribution, which has been reported for larval barnacles (*Tapia et al.*, 2010), can also influence stage-specific vulnerability of larvae by affecting the realized concentration of larval prey to predators. Temporal variability in the depth integrated abundance of predators and prey is influenced by phenology on large time scales and patchiness on short time scales. The low daily variability of the abundance of barnacle nauplii and *P. pileus* and the number of barnacle nauplii in the pharynx that I observed in 2015 suggest that weekly sampling in 2014 was adequate for resolving temporal variability in predation rates.

A limitation to this study was that predation by only a single predator was evaluated. I therefore obtained rough approximations of the predation rate of 2 other predators (*Sarsia* sp. and *T. discuadatus*) by multiplying predictions of the ingestion rate of barnacle nauplii from published laboratory-derived functional response models (*Uye and Kayano*, 1994; *Hansson and Kiørboe*, 2006) by the ratio of the concentrations of each predator and barnacle nauplii from this study. Using this method I estimate that predation rates of barnacle nauplii from *Sarsia* sp. were on the order of 0 to 0.001 d^{-1} and those from *T. discaudatus* were on the order of 0.001 d^{-1}. The ingestion rate models reported by *Hansson and Kiørboe* (2006) and *Uye and Kayano* (1994) are based on different species of predator and prey and higher prey concentrations and temperature ranges compared to this study. They can therefore only be used as first-order approximations at best, but suggest the impact of predation by these species is also low.

The low predation rates that I estimated in this study are consistent with the previous suggestion that predation may not be a major source of larval mortality (*Johnson and Shanks*, 2003). However, it is not possible to determine the importance of predation to mortality in this study because the overall mortality rate and the predation rate integrated over the entire predator community were not measured. For example, ingestion from adult planktivorous fish and benthic predators, which were not enumerated, may be important sources of predation (*Gaines and Roughgarden*, 1987; *Navarrete and Wieters*, 2000). The few measurements of predation rates of planktonic larvae integrated over predator communities are highly variable, ranging from ≤ 0.07 d^{-1} (*Johnson and Shanks*, 2003) to well over 1 d^{-1} (*Olson and McPherson*, 1987; *Allen and McAlister*, 2007). *Vaughn and Allen* (2010) point out that it is difficult to determine whether this variability is due to

methodological differences between studies or spatial and temporal variation in predation.

My results are limited to the Northwest Arm. Spatial variation in the abundance of prey and composition of predator species can lead to large variability in estimates of predation rate. For example, *Hansson et al.* (2005) found that estimates of predation rates of barnacle nauplii by *A. aurita* ranged from 0.006 to 0.99 d^{-1} and 0.02 to 2.31 d^{-1} from 2 separate surveys (n = 12 sites $survey^{-1}$) in Limfjorden, Denmark. *Pepin et al.* (2002) found that variation in larval fish mortality among sites was positively related to differences in the abundance of pelagic fish predators. Also, *Acosta and Butler* (1999) demonstrated that predation on lobster larvae was significantly higher in reef habitats rather than in lagoon or bay habitats. In the region, the highest biomass of chaetognaths is restricted to waters overlying deep basins (*Sameoto*, 1973). Therefore, the potential effect of chaetognath predation on larval barnacle populations is probably stronger in Bedford Basin and St. Margarets Bay, which are adjacent to and much deeper than the Northwest Arm.

4.5.3 Sources of variation in ingestion rates

On each sampling date, the distribution of the number of larval barnacles retrieved from the pharynx of individuals of *P. pileus* was highly skewed. I expected that the size distribution of *P. pileus* would be a potential source of this variation as a positive relationship between ctenophore size and clearance rate has been demonstrated in the laboratory (*Gibbons and Painting*, 1992). However, in this study a significant positive relationship between ctenophore size and pharynx content was only detected on 4 of the 10 sampling dates. On only one of these sampling dates, the size of ctenophores collected by dipping from floating docks was significantly higher than plankton tows. Therefore, the size bias that occasionally occurred in ctenophore collections probably had little influence on estimates of ingestion rates.

Other potential sources of variability in the pharynx content of *P. pileus* include feeding activity, prey concentration, and digestion time. When actively feeding, I expect that ctenophores exposed to higher prey concentrations over their digestion time ($\approx$ 8 h) should have more prey in their pharynx. Individual ctenophores collected on the same date may experience different prey densities over the time scale of the digestion time due to the combined effect of vertical migration and small-scale patchiness of prey. The digestion time of *P. pileus* may be influenced by ctenophore size, prey composition, and starvation. *Harris et al.* (1982) reported no relationship between digestion time of copepods and

size of *P. pileus*, but did not provide the size range tested. The presence of copepods and cyprids in the pharynx of *P. pileus* may have affected the digestion time of barnacle nauplii. I did not test for the effect of alternative prey on the digestion time; however, I demonstrated that digestion time did not vary with meal size of barnacle nauplii. This suggests that the presence of other prey items (copepods and barnacle cyprids) did not substantially affect the digestion time of barnacle nauplii within the range of meal sizes in digestion experiments.

The presence of zooplankton other than barnacle nauplii could have reduced the ingestion rate on barnacle nauplii by satiating *P. pileus*. In the laboratory, the ingestion rate of *Pleurobrachia* spp. increases linearly with the concentration of copepod prey up to $\approx$ 60 prey l^{-1} (*Reeve and Walter*, 1979; *Chandy and Greene*, 1995). In this study, the maximum concentration of barnacle nauplii was $\approx$ 10 larvae l^{-1}. I did not quantify copepod concentrations in this study; however, in Bedford Basin, *Matsakis and Conover* (1991) found that copepod (> 200 μm) concentrations ranged between 1 and 10 ind. l^{-1} during March and April. It is therefore unlikely that prey concentrations were high enough to satiate *P. pileus*. This is further supported by my observation that the pharynx of individuals of *P. pileus* was never full in this study. However, I acknowledge that the presence of other zooplankton may reduce the feeding rate of *P. pileus* without filling the pharynx. For example, it has been suggested that ctenophores reduce their feeding rate to maintain a certain number of prey items within the pharynx (*Rowe*, 1971). It has also been suggested that ambient plankton reduce feeding rates on other zooplankton by interfering with prey detection (*Johnson and Shanks*, 1997).

My estimates of ingestion rate require the determination of digestion time and involve several assumptions. Firstly, the ingestion and digestion rates (prey d^{-1}) are assumed equal (*Bromley*, 1994). Ingestion rates are therefore only accurate if ctenophores have been feeding for a sufficiently long period to reach steady state prior to collection. This assumption inherently requires that the digestion rate is not constant, but varies positively with ingestion rate. My observations indicate that digestion rate increases with meal size, and therefore support this assumption. This relationship may not hold when the number of nauplii in the pharynx of *P. pileus* exceeds the maximum meal size tested in experiments (12 nauplii), which occurred on many occasions in this study. For example, *Rowe* (1971) found a non-linear relationship between digestion rate of *P. pileus* and prey

concentration (nauplii of *Artemia* sp.) that was consistent with the Michaelis-Menten saturation curve. If the presence of many prey items (including copepods and cyprids) does indeed reduce digestion rate, this would result in an overestimate of ingestion rate. This further emphasizes that predation rates on barnacle nauplii by *P. pileus* were low in this study.

Secondly, *Bajkov* (1935)'s model assumes that digestion rate remains constant within each ctenophore as prey items in the pharynx are eliminated (*Bromley*, 1994). However, the digestion rate of many marine organisms has been shown to decrease as food content is eliminated from the gut (see reviews by *Bromley*, 1994 and *Båmstedt et al.*, 2000). I found that the digestion rate of *P. pileus* remained constant in some cases, but decreased over time in others. It is therefore possible that I did not predict ingestion rates accurately for some individuals. When the digestion rate is non-linear, predictions of ingestion rate would be over- or underestimated at low or high pharynx content levels, respectively.

In this study, the average digestion time of barnacle nauplii by *P. pileus* ranged from 7 to 8 h at 2°C and 4 to 6.5 h at 6°C. Using a different method, *Larson* (1987) estimated that *P. bachei* digested barnacle nauplii in 4.2 h at 12 to 14°C. Although I expect digestion time to be negatively related to temperature, *Kuipers et al.* (1990) found that there was little difference in digestion time of copepods by *P. pileus* between 7 and 13°C, and that the digestion time was substantially reduced at 5°C. The digestion time of larval barnacles by *Pleurobrachia* spp. appears to be longer than that of copepods, as estimates of copepod digestion time vary between 1.2 and 3.5 h over a temperature range of 7 to 14°C (*Sullivan and Reeve*, 1982; *Harris et al.*, 1982; *Larson*, 1987; *Kuipers et al.*, 1990; *Båmstedt*, 1998).

The time required for *P. pileus* to digest cyprid larvae appears to be much longer than that for nauplii. Unfortunately, the digestion time could not be determined with certainty because almost all cyprids were egested prior to complete digestion. Egestion was not induced by prey handling following feeding, as I observed the egestion of both Stage 6 nauplii and cyprids by undisturbed individuals of *P. pileus*. Observations *in situ* can determine whether this phenomenon occurs under natural conditions. I suspect that the high frequency of egestion and long digestion time that I observed were in response to the inability of digestive enzymes of *P. pileus* to penetrate the exoskeleton of the cyprid. The exoskeleton encloses the cyprid, except for a narrow opening on the ventral side, which can be tightly shut by an adductor muscle (*Walley and Rees*, 1969).

Ctenophores and cnidarian medusae have been observed egesting undigested fish eggs (*Jaspers et al.*, 2011; *Purcell et al.*, 2014). Cnidarian medusae have also been observed egesting live bivalve larvae (*Purcell et al.*, 1991). Barnacle cyprids and nauplii were frequently observed swimming freely after being egested; however, in many instances undigested larvae were egested as a bolus, in which case, if unable to free themselves, these larvae would eventually die. Although my results suggest that some undigested Stage 6 nauplii of *S. balanoides* may be egested after feeding, I assumed all nauplii found in the pharynx would be eventually fully digested.

4.6 Conclusions

In this study, larval barnacle populations were not strongly affected by predation by *P. pileus*; however, larval predation could be significant when integrated across numerous pelagic and benthic predators. Studies of predation of benthic marine invertebrate larvae are scarce, and further investigations are required to improve the ability to predict predation rates based on the community composition of predators. Future studies using ingestion models should recognize and evaluate the assumptions by making direct measurements ($i.e.$, digestion time). Also, predation rates should be quantified at several times during the larval duration and at the highest possible taxonomic resolution. I have made a first attempt at addressing these issues, and my results suggest that further studies such as this are warranted to accurately assess the importance of predation on mortality of larval benthic marine invertebrates.

CHAPTER 5

CONCLUSION

The objective of this thesis was to improve the ability to predict the ecological significance of predation on the mortality of planktonic larval stages of marine benthic invertebrates. This thesis has contributed observations from computational, laboratory, and field approaches that have facilitated the development of hypotheses on (1) the influences of larval motility and temperature on the predation process (Figure 1.1), and (2) the potential impact of predation on larval populations. I have demonstrated how the probability of encounter with a predator can be affected by directional persistence in the movement of prey, and that directional persistence of zooplankton can be affected by temperature. My observations of predation on larval barnacles by a planktonic carnivore suggest that predation in the pelagic environment may not always be detrimental to larval populations as is often assumed. In a review of the literature, I showed that quantitative data on predation of larval marine benthic invertebrates is scarce. A larger data set on predation on larval fish indicates that predation may indeed be a substantial source of larval mortality in certain instances.

In **Chapter 2**, I developed an individual based model to describe how the maximum clearance rate, F, of a motionless predator varies with the distance in which the predator can detect prey and the persistence length ($i.e.$, run length of a random walker) in the movement of the prey. The maximum clearance rate is an important metric that influences the rate of encounters of a predator with prey and the instantaneous mortality rate of the prey, assuming that all prey encountered are ingested (as outlined in **Chapter 1**). Using simulations from my model, I demonstrated that classic ("diffusive" or "ballistic") formulae overestimate F when their assumptions of movement are invalid. I also mapped

variability in F over a range of distances of prey perception and persistence length relevant to mesozooplankton, and evaluated the utility of previously proposed mathematical corrections to the classic models. **Chapter 2** highlights the need for future modelling studies on the potential interactions between directional persistence in prey movement, and prey handling time, prey susceptibility, and predator movement on clearance and encounter rates.

In **Chapter 3**, I measured directional persistence of different stages of larval barnacles in the laboratory, and demonstrated that temperature can influence the persistence length of larvae by its effect on the persistence time and swimming speed. Based on the results from my study, I predict that the probability of encountering a predator increases with increasing temperature for late stage nauplii and decreases with increasing temperature for cyprids. I also observed that nauplii had higher persistence lengths than cyprids, and suggest that predation risk may be an important mechanism influencing differences in motility patterns of feeding and non-feeding stages. Future work explicitly testing the null hypothesis of no difference in the persistence length of planktotrophic and lecithotrophic larvae would provide insight into the selective pressures associated with feeding and non-feeding life history strategies. The effects of temperature and life history strategy on vulnerability of prey to predators can also be evaluated in future studies using feeding incubations in the laboratory.

In **Chapter 3**, I also found that larval swimming speed, persistence time, and persistence length were greater in the vertical than the horizontal dimension. Zooplankton may be adapted to explore the vertical dimension due to their ability to control their vertical position (but not their horizontal position) under most instances in the sea. *In situ* observations of motility could confirm that zooplankton swimming is biased in the vertical dimension. Anisotropy in prey and predator motility can have a strong effect on encounter rates, as predators that swim perpendicular to the path of their prey have a higher probability of encountering prey than predators that swim parallel to the path of their prey (*Gerritsen*, 1980).

Theoretically, methods from **Chapters 2 and 3** can be combined to produce quantitative predictions of encounter rates for a given concentration and prey, assuming that persistence lengths are accurately measured in 2D, prey are homogenously distributed, and that the swimming paths observed in the laboratory are random and isotropic. Given the number

of assumptions and their associated uncertainties, I caution the use of persistence lengths reported in **Chapter 3** for prediction of encounter rates.

In **Chapter 4**, I used observations from the field and laboratory, in concert with gut evacuation and population models to show that the predation impact on larval barnacles by a ctenophore, *Pleurobrachia pileus*, is negligible, primarily due to the low concentration of predators relative to the concentration of larval prey. The potential impact of other pelagic predators that I identified also appeared to be low. Future research is required to identify potentially important predators and quantify their impacts on larval populations using methodological approaches such as those outlined in **Chapter 1**. In **Chapter 4**, I also demonstrated that gut contents of prey ingested whole may not always be a valid indicator of mortality due to predation, as cyprids were egested from the gut of the predator alive in the laboratory. Therefore, some larval types appear to be morphologically equipped to resist mortality post encounter (and ingestion!). *In situ* observations of egestion of larvae can confirm this hypothesis.

This thesis highlights the challenges associated with quantitatively evaluating predation using theoretical, empirical, and combined approaches, as well as the paucity of data on the mechanisms that affect encounter rates among prey and predators, and the identity and potential impact of larval predators. Challenges associated with the predation problem should not deter future research on the mechanisms that affect the predation process or the potential impact of predation on larval populations in the field. In the scientific method, observations are required for the development of hypotheses, and care should be made to make observations at relevant scales. This thesis provides observations which are sorely needed for the development of hypotheses regarding predation of marine benthic invertebrate larvae. Many concepts in this thesis can also be applied to zooplankton ecology ($i.e.$, including holoplankton). My observations support the hypotheses that predation exerts a strong selective pressure on the evolution of larval traits (such as swimming behaviour and morphological defences), but is not always detrimental to larval populations.

APPENDIX A

CHAPTER 2

A.1 Corrections to "diffusive" and "ballistic" models

Fuchs (1964) and *Harris* (1982) derived corrections to the diffusive model by quantifying the steady state diffusive flux into a radial boundary surrounding the encounter sphere. Within this boundary layer, diffusion theory ($i.e.$ Ficks law) is invalid, and the extent of the boundary layer is dependent on both λ and r (Table A.1). *Visser* (2007) proposed a correction to the ballistic model in the form of a Michaelis-Menten model (Table A.1). When converted to a correction to the diffusive model using the conversion factor $\frac{F_{Ball}}{F_{Diff}} = \frac{3r}{4\lambda}$, the *Visser* (2007) correction is $\frac{F}{F_Diff} = \frac{r/\lambda}{(4/3)+(r/\lambda)}$. When $\lambda << r$, the *Fuchs* (1964) correction reduces to essentially the same model, but with a half saturation constant of $\pi/2$ rather than $4/3$ (Table A.1).

Although a derivation of the *Visser* (2007) correction is not available, it can be derived from $\frac{F}{F_{Ball}} = 1 - \frac{F}{F_Diff}$ where F is the realized maximum clearance rate, and F_{Diff} and F_{Ball} are predicted by the diffusive and ballistic models at steady state, respectively. Therefore, the *Visser* (2007) correction assumes that F represents a balance between diffusive and ballistic components ($i.e.$ as F becomes less diffusive, it becomes equally more ballistic, and *vice versa*). The "1-correction" conversion is also inherent to the self-overlap metric of swimming trajectories developed by *Bianco et al.* (2014).

Table A.1: The diffusive and ballistic models and their corrections. Note that $\zeta = \lambda/r$. F_{Diff} refers to the steady state value 4 in Equation 2.1. *Fuchs* (1964)'s correction is adapted herein for movement of only one particle population. In the *Harris* (1982) correction, the constant C = 1/3, is required to convert the persistence length, λ, to the "boundary layer length" defined in *Harris* (1982).

Model	Formula	Reference
Fuchs correction	$\frac{F}{F_{Diff}} = \frac{1}{(r/(r+A))+(\zeta\pi/2)}$	*Fuchs* (1964)'s Equation 49.19
	$A = \frac{1}{3}((r+\lambda)^3 + (r^2+\lambda^2)^{3/2}) - r$	
Harris correction	$\frac{F}{F_{Diff}} = (\frac{4}{3\pi BC})(1 + \frac{1.85}{C\zeta})$	*Harris* (1982)'s Equation 26
	$B = \frac{0.79}{(C\zeta)^2} + \frac{2.35}{C\zeta} + 2.27$	
	$C = \frac{1}{3}$	
Visser correction	$\frac{F}{F_{Ball}} = \frac{\zeta}{0.75+\zeta}$	*Visser* (2007)'s Equation 12

A.2 Individual based model

A.2.1 Encounter criteria

I defined an encounter as the occurrence of a prey item within radial distance, r, of the origin ($i.e.$ predators center) at any point during the time step Δt. In Figure A.1, I illustrate how I used vector geometry to determine encounter criteria for a particle moving from position X_t to X_t + Δt. I defined the vector between X_t and the origin as $\vec{a}$, the vector between X and X_t + Δt as $\vec{b}$, and the vector between X_t + Δt and the origin as $\vec{c}$. Note that even if $||\vec{c}||$ is $> r$, it is possible for the particle to have come within r during (as shown). The vector $\vec{b_1}$ was calculated as:

$$\vec{b_1} = \frac{\vec{a} \cdot \vec{b}}{\vec{b} \cdot \vec{b}} \vec{b} \tag{A.1}$$

$\vec{b_1}$ is the projection of $\vec{a}$ onto $\vec{b}$ ($i.e.$ the "shadow" of $\vec{a}$ onto $\vec{b}$) such that the vector $\vec{e} = \vec{a} - \vec{b_1}$ is orthogonal to $\vec{b}$. $||\vec{e}||$ is the shortest distance between the prey path and the origin; therefore, an encounter occurs when $||\vec{e}|| < r$.

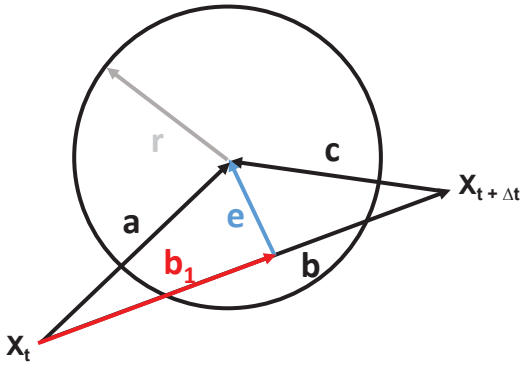

Figure A.1: Vector geometry used to derive encounter criteria. See text for description of symbols.

A.2.2 MATLAB code

A.2.2.1 Main code

```
%This code simulates the time-varying encounter rate between prey with correlated random walk
%motility and a motionless predator with a spherical perceptive field situated at the origin of a spherical domain

%This code requires:
%(1) "randfixedsum.m" for selecting displacements of prey in random directions within each dimension. The code is is freely
%available at https://www.mathworks.com/matlabcentral/fileexchange/9700-random-vectors-with-fixed-sum/content/randfixedsum.m
%last accessed June 14, 2017. All other components of this code were written by Kevin Sorochan and Wendy Gentleman

%(2) "repos.m" for repositioning prey that leave the domain

```

```
11 %In addition, "shell.m" can be used to determine the
       initial and final concentration of
12 %particles within bins of a specified width and radial
       distance from the
13 %origin of the domain
14
15 clear
16 close all
17
18 %Initialization (currently set up for "short simulation")
19 dt = .1; %Time step [s]; the time step should not exceed
       the minimum value of the persistence time, tau
20 DT = 3; %Duration of simulation [s]
21 n = 3; %Number of dimensions
22 speed = .001; %Speed of prey [m/s];
23 disp = speed*dt; %Distance travelled by prey over one time
       step [m]
24 concentration = 2.5*(1e3)*(1e9); %Concentration of prey
       within domain. The factor (1e9) converts [prey/mm^3] to
       [prey/m^-3]; AD
25
26 %Specify values of persistence time, tau, and prey
       perception distance, r
27 %for simulations
28 for i = 2;
29 tau = i; %Persistence time(s) [s]
30
31
32 for ii = 0.0005;
33 r = ii; %Reaction distance(s) of predator [m]
34
35 %Determine number of particles for specified concentration
```

```
36 constant = 5; %Define factor used to determine the radius
       of the domain
37 R = constant*r; %Compute radius of domain [m]
38 v = (4/3)*(pi)*(R^3); %Compute volume of domain [m^3]
39 n_part_init = round(concentration*v); %Number of prey
       required to satisfy specified concentration
40 n_part = n_part_init;
41
42 t = 0; %Set initial time
43 n_sim = 0; %Set initial simulation number
44
45 diffusivity = ((speed^2)*tau)/n; %Update diffusivity [m^2/s
       ]
46 temp = (1:n_part)'; %This vector is used as an alterative
       to the function, find()
47
48 %Predator position (at origin of domain)
49 X_pred_repeat = zeros(n_part, 3);
50
51 %Determine prey positions from a uniform distribution
       between
52 %the inner sphere (i.e. perceptive field of the predator)
       with radius, r,
53 %and outer sphere (i.e. domain) with radius, R.
54 s_norm = randn(3, n_part);
55 radial_distance = (rand(1, n_part)*(R^3-r^3)+r^3).^(1/3);
56 c = radial_distance./sqrt(sum(s_norm.^2,1));
57 s = bsxfun(@times, s_norm, c);
58 X_init = s.';
59 X_prey_t = X_init;
60
61 %Generate matrix of prey displacements over dt
```

```
62 binary = round(rand(size(X_init))); %Generate binary matrix
       of randomly placed ones and zeros
63 binary(~binary) = -1; %Replace zeros with negative ones in
      binary matrix; this gives the direction in each
      dimention.
64 random = randfixedsum(n, n_part, disp^2, 0 , disp^2)'; %
      Generate random values of squared distances travelled in
       each dimension by the prey that add to disp^2.
65 random = sqrt(random); %Calculated the distance travelled
      in each dimension
66 DeltaX = random.*binary; % Calculate dispalcement in each
      dimension over dt (this represents vector "b" in
      Appendix 2)
67
68
69 % Determine and plot concentration of prey within equally
      spaced shells from r to R (initial)
70 n_bin = 40; %The number of bins for calculating particle
      concentration within the domain; required input into
      shell function
71 bin = (R-r)/n_bin;
72 r_bin = bin*(1:n_bin); %Quantify the length intervals that
      the concentration is calculate in
73 conc_profile_init = shell(n_bin, bin, R, r, X_prey_t, temp)
      ; %Use function "shell.m"
74
75 figure
76 scatter(1 + r_bin/r, conc_profile_init/concentration)
77 ylim([0,1.5])
78
79 hold on
80 plot(1 + r_bin/r, ones(1,n_bin))
```

```
81 hold off
82
83 %Preallocate matrices for data storage
84 t_store = zeros(round(DT/dt),1); %Time
85 e_store = zeros(round(DT/dt),1); %Number of encounters
86
87 %Time step loop
88 while t < DT
89
90     % Determine the distance between the prey and predator
       prior to moving
91     D_t = X_pred_repeat - X_prey_t; %Vector between
       predator and prey at time, t (this represents vector
        "a" in Appendix 2)
92     dist_t_sqrd = sum(D_t.*D_t,2); %Squared distance
       between predator and prey at time t
93
94     %Find individuals that change direction when t > 0 and
       update
95     %displacements
96     if ~t == 0
97         prob_newdir = 1-exp(-dt/tau); %Probability of
           changing direction
98         newdir_ind = temp(rand(n_part,1) < prob_newdir); %
           Find individuals that change direction of travel
99         binary = round(rand(length(newdir_ind), n)); %
           Create binary matrix of randomly placed ones and
            zeros
100        binary(~binary) = -1; %Replace zeros with negative
           ones
101        random = randfixedsum(n, length(newdir_ind), disp
           ^2, 0 , disp^2)';
```

```
102         random = sqrt(random); %Determine the magnitude of
                displacement in each dimension
103         DeltaX(newdir_ind,:)= random.*binary; %Randomly
                choose direction (sign) of travel in each
                dimension
104     end
105
106     %Calculate variables that are required to find
            encounters
107     mag_DeltaX_sqrd = sum(DeltaX.*DeltaX,2); %Distance
            between positions at time t and t + dt
108     Dt_dot_DeltaX = sum(D_t.*DeltaX,2); %Numerator in
            equation to calculate tt
109     X_prey_tplusdt = X_prey_t + DeltaX; %Prey particles at
            time t + dt
110     D_tplusdt = X_pred_repeat - X_prey_tplusdt; %Vector
            between prey and predator at t + dt
111
112     %Determine if encounter occurs (see encounter criteria)
113     tt = (Dt_dot_DeltaX)./mag_DeltaX_sqrd;
114
115     case1 = (tt>1); %Prey particle lands inside encounter
            sphere at time t + dt
116     dist1 = sum(D_tplusdt.*D_tplusdt,2);
117
118     case2 = (tt>0 & tt<=1); %Prey passes through perceptive
             sphere of predator over dt
119     dist2 = (dist_t_sqrd) + (tt.^2.*mag_DeltaX_sqrd) - (2*
            tt.*Dt_dot_DeltaX);
120
121     %Find encountered and not-encountered prey
```

```
122     encounter = ((case1 & dist1 <= r^2) | (case2 & dist2 <=
            r^2));
123     encounter_ind = temp(encounter == 1); % Find
            encountered prey
124     no_encounter_ind = temp(encounter == 0); %Find prey not
            encountered
125
126     %Move particles that will not encounter predator to new
            locations
127     X_prey_t(no_encounter_ind,:) = X_prey_tplusdt(
            no_encounter_ind,:);
128
129     %Update X_prey_t by repositioning prey that have left
            domain such that they pass through the
130     %opposite side
131     [reposition, digjump] = repos(X_prey_t, DeltaX, dt, R,
            temp);
132     X_prey_t(digjump,:) = reposition;
133
134     %Check to make sure that all particles are in the
            domain
135     [azimuth, elevation, radial_d] = cart2sph(X_prey_t(:,1)
            , X_prey_t(:,2), X_prey_t(:,3)); %Convert to
            spherical coordinate system
136     digjump2 = temp(radial_d > R); %Find prey that remain
            outside domain
137
138     %If prey are found outside of domain, set radial
            distance to R
139     if length(digjump2 > 0)
140
```

```
141             new_radial_d = radial_d(digjump2,:)*0 + R; % set
                    radial distance to boundary
142             new_azimuth = azimuth(digjump2,:);
143             new_elevation = elevation(digjump2,:);
144             [X, Y, Z] = sph2cart(new_azimuth, new_elevation,
                    new_radial_d);
145             X_prey_t(digjump2,:) = [X, Y, Z];
146
147         end
148
149         %Eliminate encounterd prey
150         X_prey_t(encounter_ind,:) = [];
151         X_pred_repeat(encounter_ind,:) = [];
152         DeltaX(encounter_ind,:) = [];
153
154         n_part = length(X_prey_t); %Update the number of
                particles in the domain
155
156         %Increment number of simulations
157         n_sim = n_sim+1;
158
159         %Increment time
160         t = t+dt;
161
162         %Store time
163         t_store(n_sim,1) = t;
164
165         %Store number of encounters
166         e_store(n_sim,1) = length(encounter_ind);
167
168 end
169
```

```
170     %Determine and plot concentration of prey within
            equally spaced shells
171     %from r to R (at DT)
172     conc_profile_DT = shell(n_bin, bin, R, r, X_prey_t,
            temp); %Use function "shell.m"
173
174     figure
175     scatter(1 + r_bin/r, conc_profile_DT/concentration)
176     ylim([0,1.5])
177
178     hold on
179     plot(1 + r_bin/r, ones(1,n_bin))
180     title(sprintf('tau = %d,r = %d', i, ii*1000)) % tau in
            seconds and r in mm in plot title
181     hold off
182
183
184     %Calculate clearance rates from tabulated encounters
185     beta = (e_store)*v/((dt)*n_part_init); %Clearance rate
            [m^3/s]
186     beta = beta*1E9; %Clearance rate [mm^3/s]
187
188     %Solutions of clearance rate from diffusive and
            ballistic models
189     beta_diff = (4*pi*r*diffusivity); %Calculate clearance
            rate [mm^3/s] from diffusive model at steady state (
            i.e. Koch, 1960)
190     beta_diff_time = beta_diff*(1 + r./((pi*diffusivity*
            t_store).^0.5))*1E9; %Calculate time-varying
            clearance rate [mm^3/s] from diffusive model (i.e.
            Koch, 1960)
```

```
191     beta_ball = (pi*(r^2)*speed)*1E9; %Calculate clearance
            rate [mm^3/s] from ballistic model (i.e. Gerritsen
            and Strickler, 1977)
192
193     %Creat vectors
194     beta_diff_mat = repmat(beta_diff, length(t_store), 1)*1
            E9; % values of diffusive clearance rate [mm^3/s]
195     beta_ball_mat = repmat(beta_ball, length(t_store), 1);
            %Repeated values of ballistic clearance rate [mm^3/s
            ]
196
197     %Plot data for each combination of r and tau
198     figure
199     plot(t_store, beta, 'k', t_store, beta_diff_time, 'r',
            t_store, beta_diff_mat, 'm', t_store, beta_ball_mat
            , 'g')
200
201 end
202 end
```

A.2.2.2 Required functions

```
1 function [X_R_repos, digjump] = repos(X_prey_t, DeltaX, dt,
      R, temp)
2
3 %This function computes the component of the displacement
      of a prey item
4 %outside of the domain. This displacement compontent is
      then used to move
5 %the prey item into the domain on the opposite side.
6
7 %The compontent of displacement is solved by first finding
      the time
```

```
%required for the prey item to reach the domain edge (i.e. t1_dj). Then
%time after leaving the domain is calculated by subtracting t1_dj from the
%time step, dt (i.e. t2 = dt - t1_dj).

%t1_dj is solved for by finding the time that satisfies the condition:
%X^2 + Y^2 + Z^2 = R^2, where X, Y, Z = initial position + velocity*t1_dj

X_prey_t_not = X_prey_t - DeltaX; % get matrix of initial positions (one timestep prior)

v_prey = DeltaX/dt; % get matrix of velocities

a = sum(v_prey.*v_prey,2); % get squared magnitude of velocities ||v_prey||^2

b = 2*(sum(X_prey_t_not.*v_prey,2)); % get 2 x dot product of positions and velocities

c = sum(X_prey_t_not.*X_prey_t_not,2) - R^2; % get squared magnitude of positions ||X_prey_t||^2

num1 = -1*b; % first term in numerator of quadratic equation

num2 = (b.^2) - 4*(a.*c); % second term in numerator of quadratic equation

denom = 2*a; % get denominator for quadratic equation
```

```
30
31 num_plus = num1 + (num2).^0.5; % get numerator for
       quadratic equation 1
32
33 num_minus = num1 - (num2).^0.5; % get numerator for
       quadratric equation 2
34
35 t1 = num_plus./denom; % get time travelled to domain edge (
       i.e. R)
36
37 t_minus = num_minus./denom; % these are negative times and
       are therefore invalid
38
39 digjump = temp(t1 < dt & t1 > 0); % get rows in which prey
       have have left the domain
40
41 t1_dj = t1(digjump,:); % get time travelled before leaving
       domain
42
43 t2 = dt - t1_dj; % get time travelled after leaving domain
44
45 X_R_minus = (X_prey_t_not(digjump,:) + (v_prey(digjump,:)
       .*[t1_dj t1_dj t1_dj]))*-1; % get position at domain
       edge and move to opposite side of domain
46
47 X_R_repos = X_R_minus + (v_prey(digjump,:).*[t2 t2 t2]); %
       get final positions after adding the remaining distance
       travelled
48
49 end
```

```
1 function c_shell_store = shell(n_bin, bin, R, r, X_prey_t,
      temp)
```

```
2
3 %Convert X_prey_t from cartesian to spherical coordinate
    system
4 [azimuth_pos, elevation_pos, radial_pos] = cart2sph(
    X_prey_t(:,1), X_prey_t(:,2), X_prey_t(:,3));
5
6 %Determine how many particles are within different shells
7 npart_shell_store = zeros(n_bin, 1);
8 v_shell_store = zeros(n_bin,1);
9 c_shell_store = zeros(n_bin,1);
10
11 for i = 1:n_bin
12 bin_mat_sphere = temp(radial_pos < (r + bin*i)); %Find prey
    in sphere of interest
13 bin_mat_sphere_last = temp(radial_pos < (r + bin*(i-1))); %
    Find prey in last inner sphere
14 npart_sphere = length(bin_mat_sphere(:,1)); %Count number
    of prey in sphere
15 npart_sphere_last = length(bin_mat_sphere_last(:,1)); %
    Count number of prey in last inner sphere
16 npart_shell = npart_sphere - npart_sphere_last; % Compute
    number of prey in outer shell
17 v_sphere = (4/3)*pi*(r + bin*i)^3; %Compute volume of
    sphere of interest
18 v_sphere_last = (4/3)*pi*(r + bin*(i-1))^3; %Compute volume
    of last inner sphere
19 v_shell = v_sphere - v_sphere_last; % Compute volume of
    outer shell
20 c_shell = npart_shell/v_shell; % Compute concentration of
    prey in outer shell
21 npart_shell_store(i,1) = npart_shell;
22 v_shell_store(i,1) = v_shell;
```

```
23 c_shell_store(i,1) = c_shell;
24 end
25
26 end
```

A.2.3 Time varying clearance rate at low prey concentration

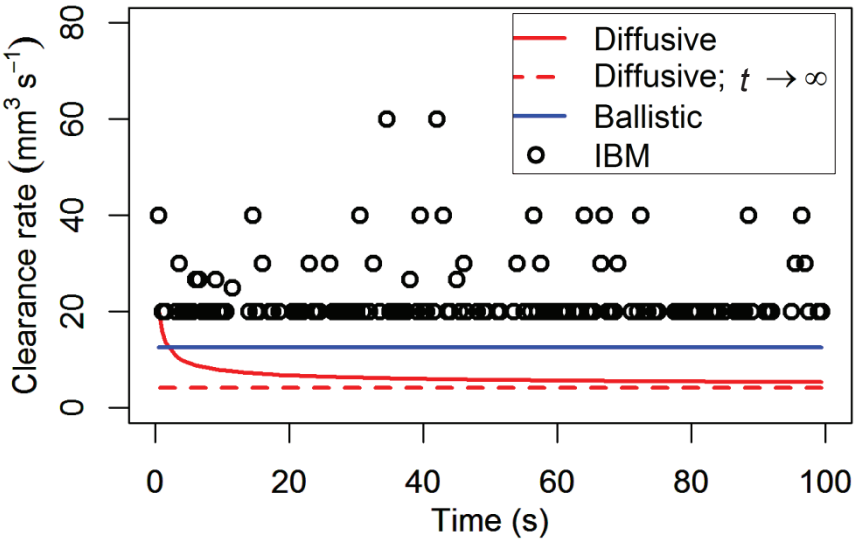

Figure A.2: Time series of the maximum clearance rate ($\lambda = 0.5$ mm, $r = 2$ mm) at low prey concentration (0.1 prey mm^{-3}).

APPENDIX B

CHAPTER 3

B.1 Curve fits

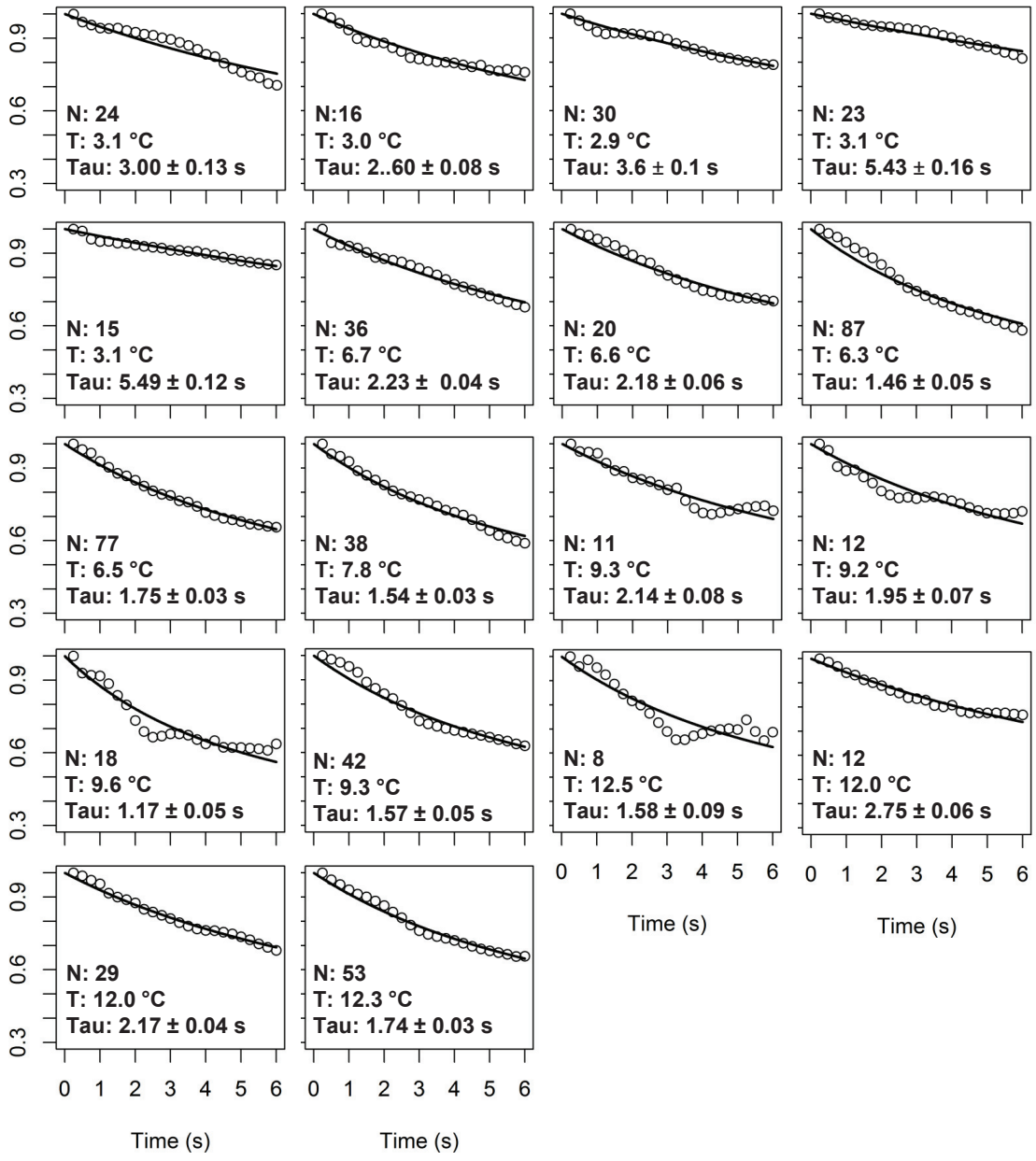

Figure B.1: Relationships between the ratio of rms distance to gross distance travelled (in the xz plane) and time for each video recording of Stage 2 nauplii. The open circles represent the data, and the black line represents the curve fit from the correlated random walk model (Equation 3.2), from which the persistence time, Tau, was estimated. Within each panel, the sample size (N), temperature (T), and estimated persistence time (Tau $\pm$ SE) are specified.

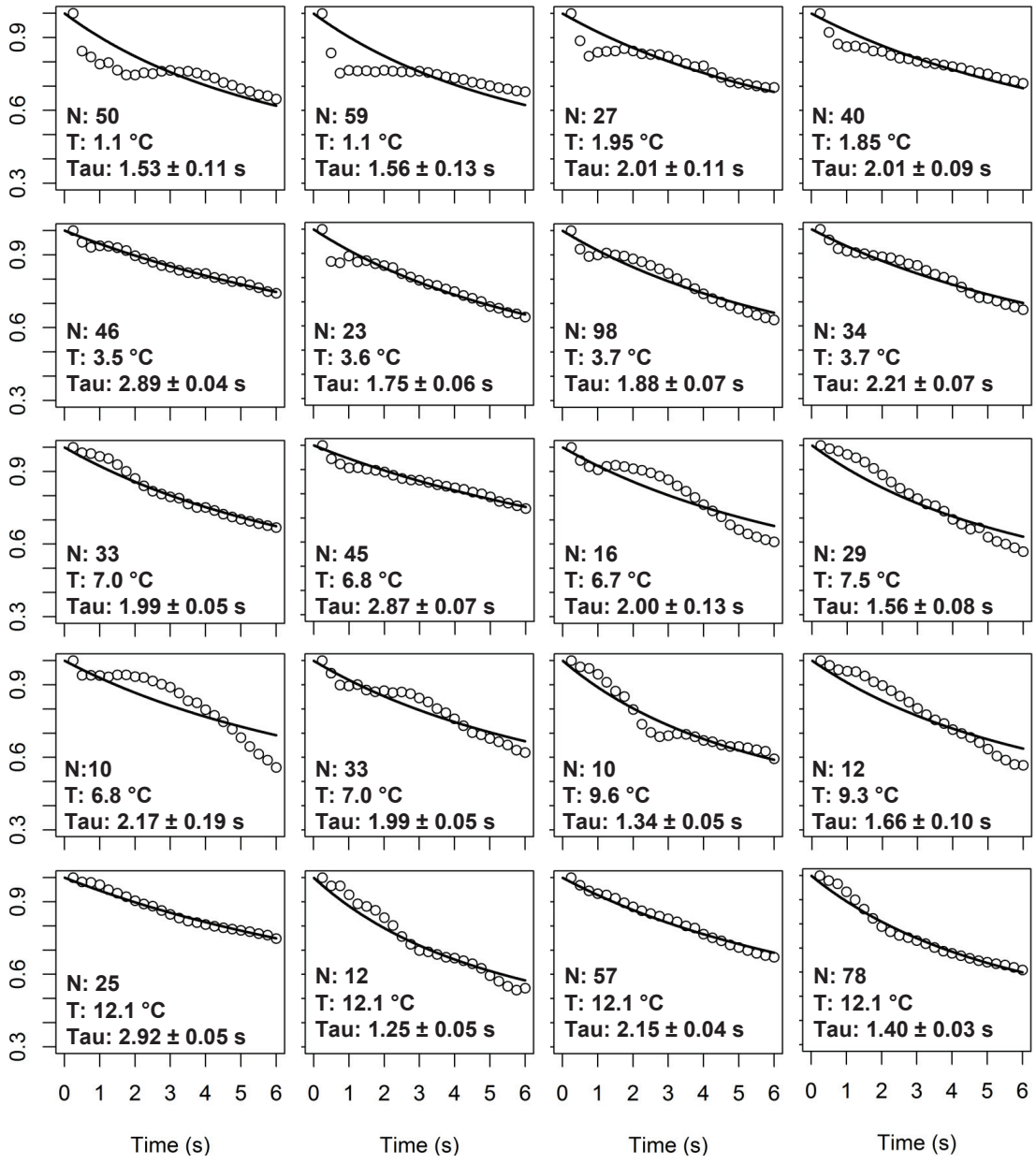

Figure B.2: Relationships between the ratio of root mean squared distance to gross distance travelled (in the xz plane) and time for each video recording of Stage 6 nauplii. The open circles represent the data, and the black line represents the curve fit from the correlated random walk model (Equation 3.2), from which the persistence time, Tau, was estimated. Within each panel, the sample size (N), temperature (T), and estimated persistence time (Tau $\pm$ SE) are specified.

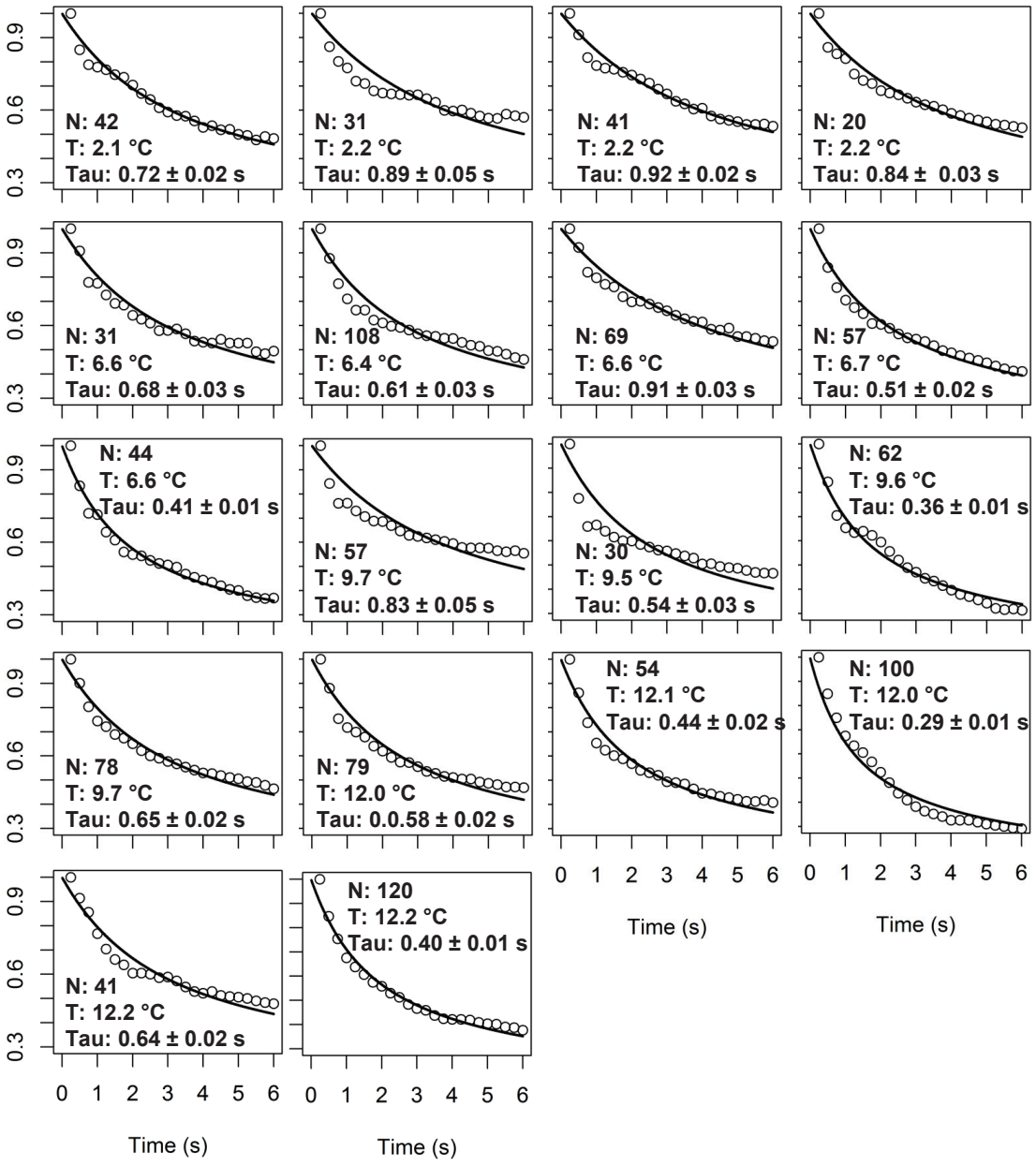

Figure B.3: Relationships between the ratio of root mean squared distance to gross distance travelled (in the xz plane) and time for each video recording of cyprids. The open circles represent the data, and the black line represents the curve fit from the correlated random walk model (Equation 3.2), from which the persistence time, Tau, was estimated. Within each panel, the sample size (N), temperature (T), and estimated persistence time (Tau $\pm$ SE) are specified

B.2 Correlation coefficients from path subsets

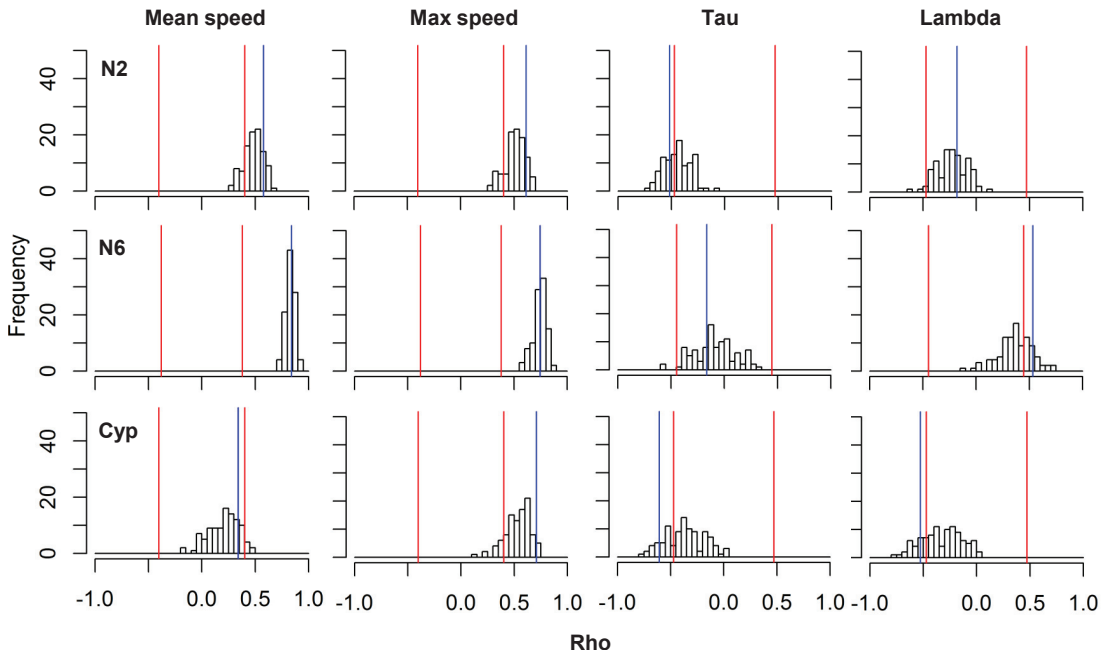

Figure B.4: The distribution of Spearman rank coefficients (Rho) obtained from the relationship between swimming metrics (difference between z and x components of the mean and maximum swimming speed, and ratios of the net displacement to gross distance travelled in the x and z directions) and temperature from 100 subsets of paths for each Stage (second nauplius, N2, sixth nauplius, N6, and cypris, Cyp). The number of paths within each path subset was set as the minimum number of paths observed from a video-recording in the stage of interest. The red lines indicate critical values of Rho, whereas the blue line indicates the value of Rho obtained using all available paths.

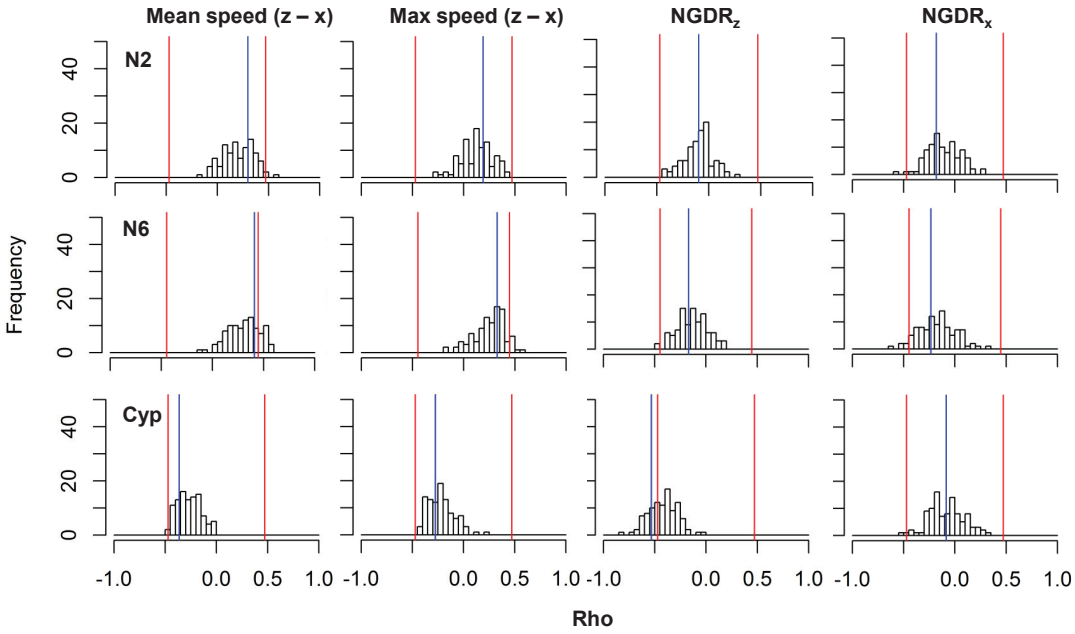

Figure B.5: The distribution of Spearman rank coefficients (Rho) obtained from the relationship between swimming metrics (difference between z and x components of the mean and maximum swimming speed, and ratios of the net displacement to gross distance travelled in the x and z directions) and temperature from 100 subsets of paths for each Stage (second nauplius, N2, sixth nauplius, N6, and cypris, Cyp). The number of paths within each path subset was set as the minimum number of paths observed from a video-recording in the stage of interest. The red lines indicate critical values of Rho, whereas the blue line indicates the value of Rho obtained using all available paths.

APPENDIX C

CHAPTER 4

Table C.1: Number of ctenophores collected in April 2015 and mean ± SD number of barnacle nauplii and copepods retrieved from the pharynx of *Pleurobrachia pileus*.

Date	**Dip time (h)**	***P.pileus* (n)**	**Barnacle nauplii**	**Copepods**
2015-04-06	18:00	42	0.50 ± 1.78	1.23 ± 2.09
2015-04-07	06:00	23	0.70 ± 1.49	2.83 ± 3.39
2015-04-15	15:00	32	0.06 ± 0.25	0.25 ± 0.80
2015-04-16	06:30	43	0.05 ± 0.21	1.16 ± 2.47

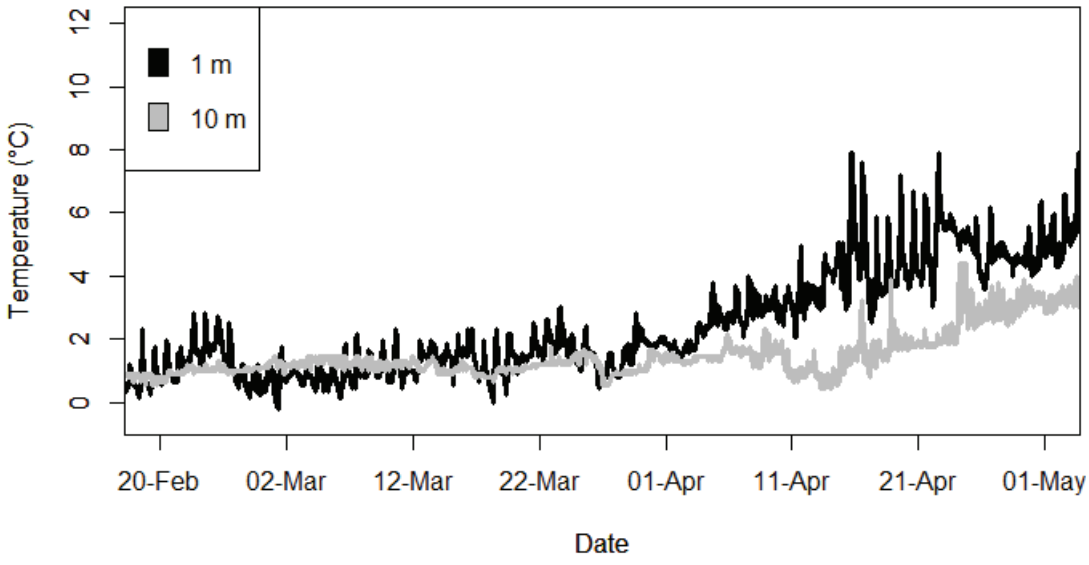

Figure C.1: Time series of temperature 1 m and 10 m from a buoy in the Northwest arm at site 1 over the sampling period.

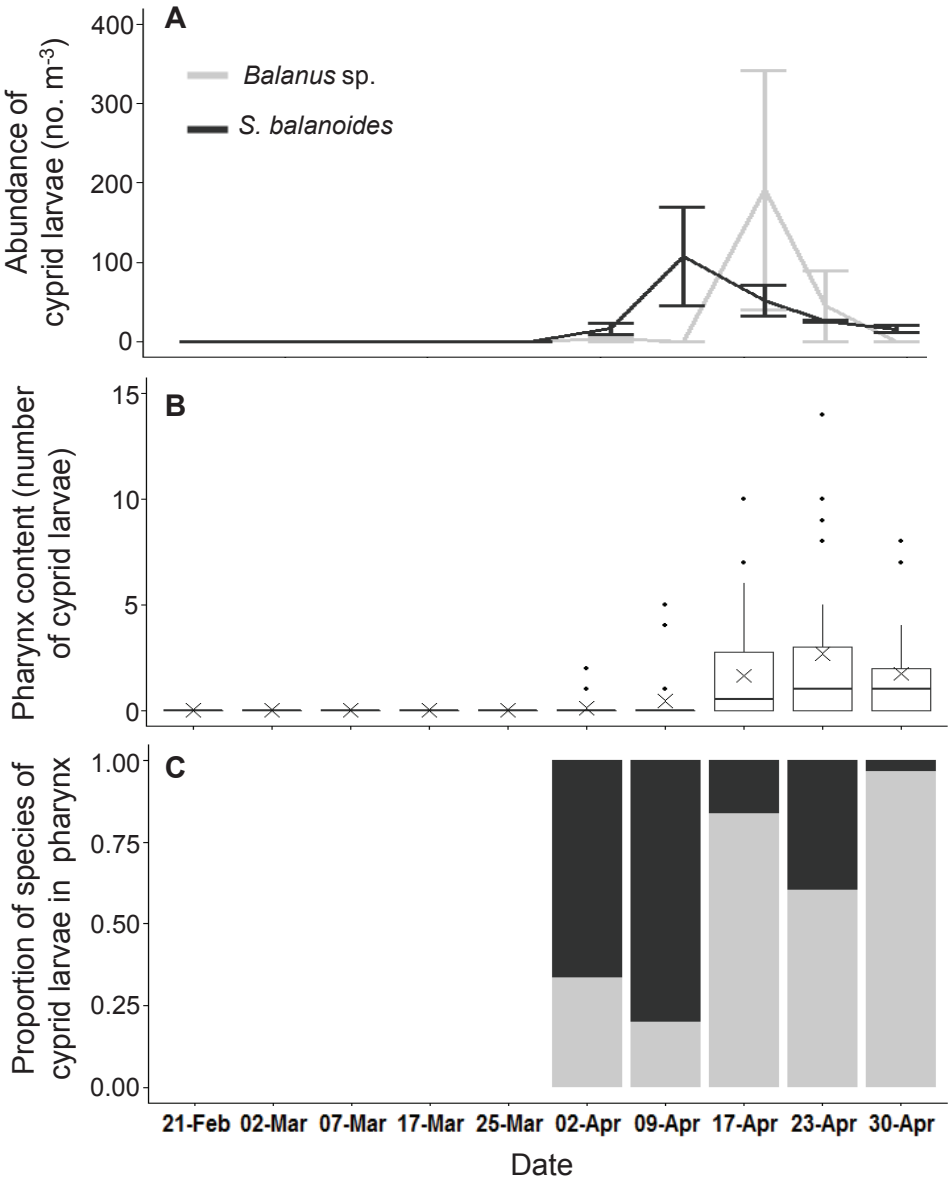

Figure C.2: Time series of (A) average (± 1 SE; n = 2) concentrations of cyprids of *Balanus* sp. and *Semibalanus balanoides* (B) barnacle cyprids (species combined) in the pharynx of ctenophores (Box plots; median ± interquartile range [IQR]; whiskers 1.5 IQR; X symbol denotes mean) and (C) the proportion of barnacles recovered from the pharynx of ctenophores catagorized as *Balanus* sp. and *S. balanoides*.

Table C.2: Potential predators of barnacle nauplii identified from zooplankton samples taken from the Northwest Arm, NS, between 21 Feb and 30 Apr 2014. Grey shading indicates the timing of presence for each predator.

Phylum	**ID**	**Date (day, month)**									
		21 Feb	2 Mar	7 Mar	17 Mar	25 Mar	2 Apr	9 Apr	17 Apr	23 Apr	30 Apr
Annelida	Syllidae (adult)										
	Tompteridae										
Arthropoda	Gammeridae										
	Hyperidae										
	Cumacea										
	Centropages sp.										
	Tortanus discaudatus										
	Anomura zoeae										
	Brachyura zoeae										
	Pandalidae zoeae										
	Other shrimp zoeae										
Chaetognatha	*Parasagitta elegans*										
Cnidaria	*Aglantha digitale*										
	Bougainvilla sp.										
	Clytia sp.										
	Hybocobon sp.										
	Rakthea octopunktata										
	Sarsia sp.										
	Scyphozoan ephyra										
Chordata	Clupeidae										
	Gadidae										
Ctenophora	*Pleurobrachia pileus*										

Table C.3: Test statistics from χ^2 tests comparing prey frequency in the pharynx of *Pleurobrachia pileus* and the water column. At α = 0.05, $\chi^2_{critical}$ = 3.84. Selectivity index, β.

Date	***B. balanus***		***B. crenatus***		***S. balanoides***	
	χ^2	β	χ^2	β	χ^2	β
2014-02-21	9.93	0.08	2733.97	0.78	4925.92	0.14
2014-03-02	76.46	0.38	85.52	0.29	292.74	0.34
2014-03-07	128.68	0.18	59.14	0.67	207.26	0.14
2014-03-17	8.76	0.30	331.23	0.53	17.42	0.16
2014-03-25	269.21	0.41	19.92	0.51	31.28	0.08
2014-04-02	0.56	0.30	346.59	0.57	50.11	0.13
2014-04-09	52.84	0.16	253.98	0.81	80.69	0.02
2014-04-17	46.82	0.14	296.73	0.76	8.39	0.10
2014-04-23	335.97	0.22	1545.88	0.57	110.24	0.20
2014-04-30	4.00	0.34	601.04	0.64	25.60	0.02
Pooled data	**179.07**	**0.11**	**2258.53**	**0.83**	**150.24**	**0.06**

Table C.4: Results from regressions between average digestion time and meal size for experiments in which individuals of *Pleurobrachia pileus* were fed multiple prey.

Experiment, temperature °C	**df**	**Coefficient**	**t-statistic**	**P**	**R^2**
2, 2	6	< 0.001	$<$-0.01	0.999	-0.167
2, 6	6	-0.036	-0.36	0.729	-0.142
3, 6	4	0.081	2.60	0.060	0.535
4, 6	5	0.046	0.451	0.671	-0.153

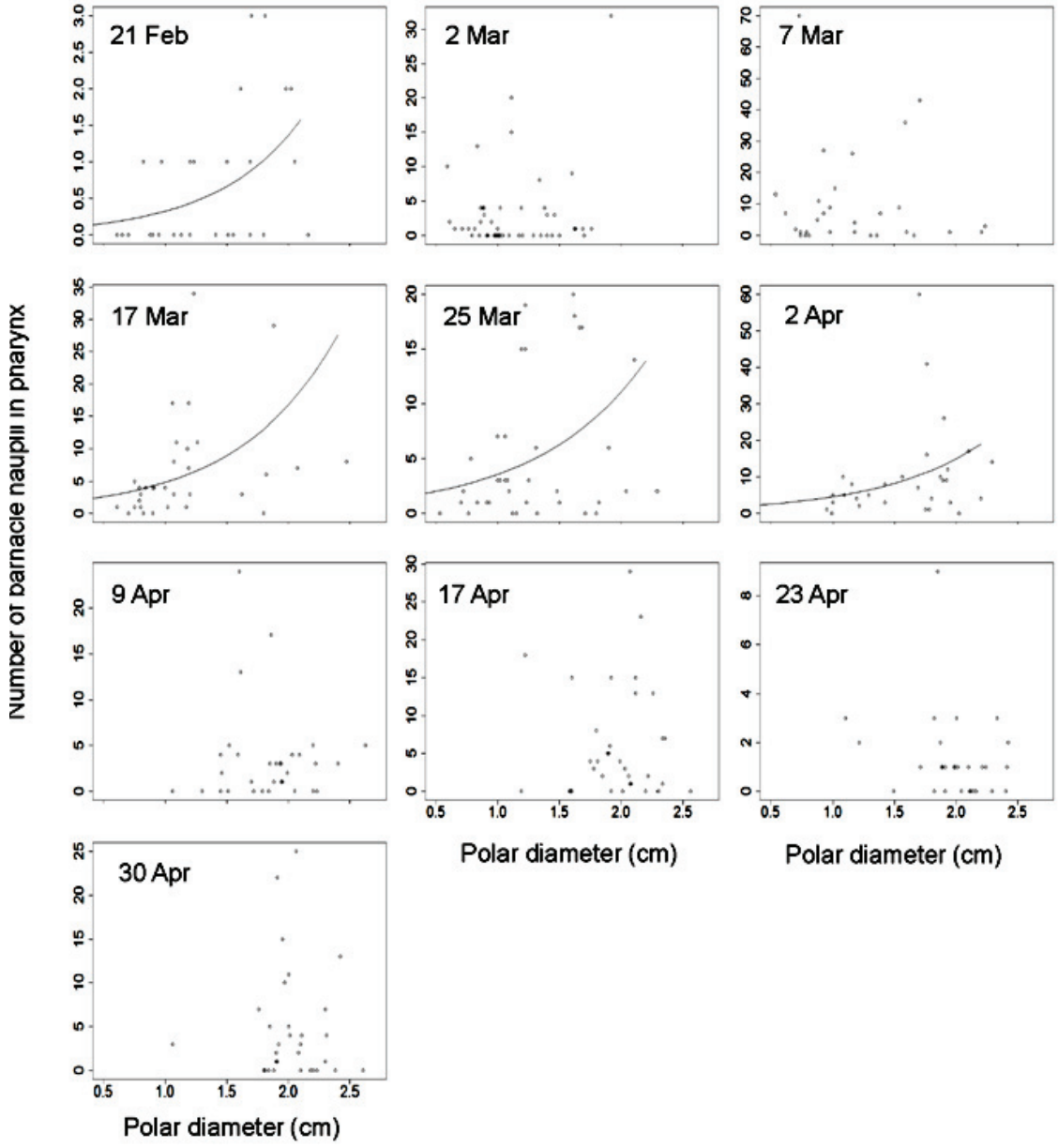

Figure C.3: The relationship between number of nauplii recovered from the pharynx and polar diameter of *Pleurobrachia pileus* for each sampling date. Fit of generalized linear model shown for significant relationships.

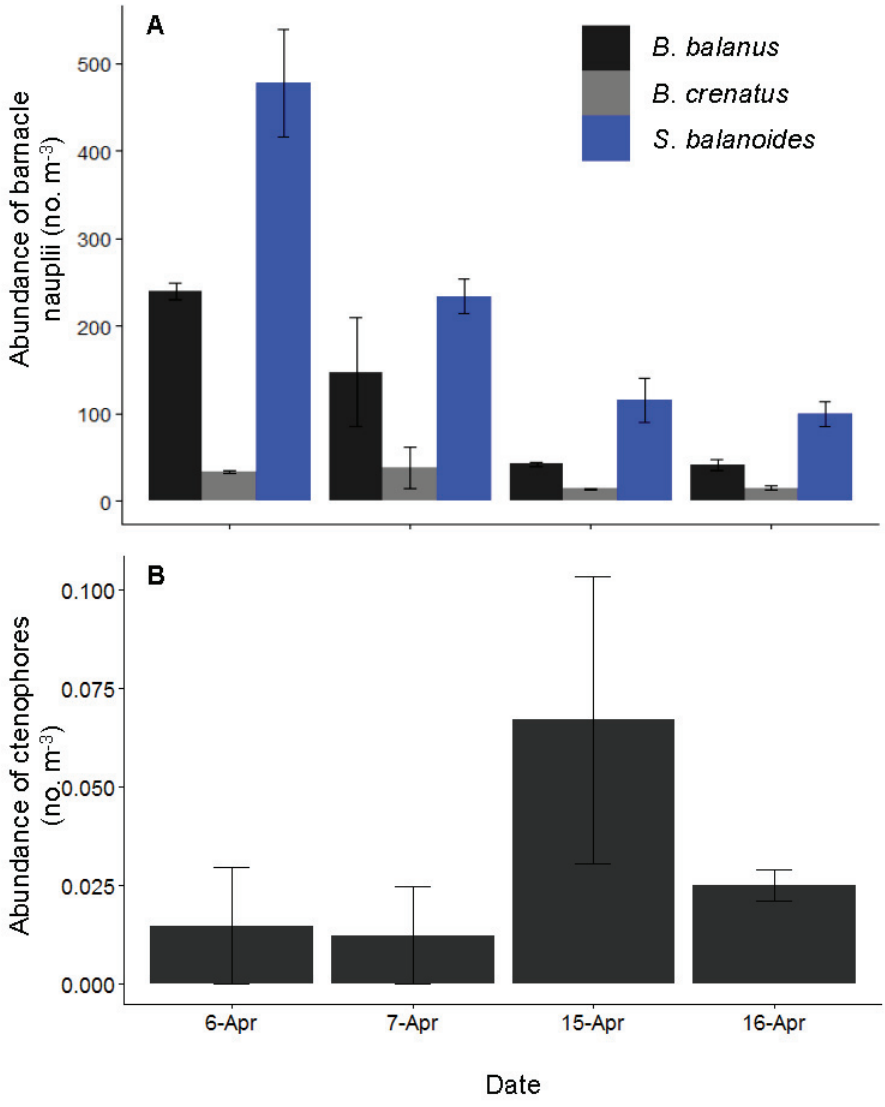

Figure C.4: Mean (± 1 SE, n = 2 sites) concentrations of (A) nauplii of *Balanus balanus*, *Balanus crenatus*, *Semibalanus balanoides* and (B) *Pleurobrachia pileus* in April 2015.

APPENDIX D

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BIBLIOGRAPHY

Acosta, C. A., and M. J. Butler, Adaptive strategies that reduce predation on caribbean spiny lobster postlarvae during onshore transport, *Limnology and Oceanography*, *44*, 494–501, 1999.

Aksnes, D. L., and M. D. Ohman, A vertical life table approach to zooplankton mortality estimation, *Limnology and Oceanography*, *41*, 1461–1469, 1996.

Allen, J. D., and J. S. McAlister, Testing rates of planktonic versus benthic predation in the field, *Journal of Experimental Marine Biology and Ecology*, *347*, 77–87, 2007.

Alvarez-Cadena, J. N., Feeding of the chaetognath sagitta elegans verrill, *Estuarine, Coastal and Shelf Science*, *36*, 195–206, 1993.

Ambler, J. W., and B. W. Frost, The feeding behavior of a predatory planktonic copepod, *Tortanus discaudatus*, *Limnol. Oceanogr*, *19*, 446–451, 1974.

Anderson, D. T., *Barnacles: structure, function, development and evolution*, Chapman Hall, 1994.

Anderson, E., Trophic interactions among ctenophores and copepods in st. margaret's bay, nova scotia., Ph.D. thesis, Dalhousie University, 1974.

Bachiller, E., U. Cotano, L. Ibaibarriaga, M. Santos, and X. Irigoien, Intraguild predation between small pelagic fish in the bay of biscay: impact on anchovy (engraulis encrasicolus l.) egg mortality, *Marine Biology*, *162*, 1351–1369, 2015.

Bailey, K., and E. Houde, Predation on eggs and larvae of marine fishes and the recruitment problem, *Advances in marine biology*, *25*, 1–83, 1989.

Bailey, K., R. Brodeur, N. Merati, and M. Yoklavich, Predation on walleye pollock (theragra chakograrnma) eggs and yolk-sac larvae by pelagic crustacean invertebrates in the western gulf of alaska, *Fisheries Oceanography*, *2*, 30–39, 1993.

Bainbridge, V., and B. McKay, The feeding of cod and redfish larvae, *International Commission Northwest Atlantic Fishery Special Publication*, *7*, 187–217, 1968.

Bajkov, A., How to estimate the daily food consumption of fish under natural conditions, *Transactions of the American Fisheries Society*, *65*, 288–289, 1935.

Berg, H. C., *Random walks in biology*, Princeton University Press, 1993.

Berg, H. C., D. A. Brown, et al., Chemotaxis in escherichia coli analysed by three-dimensional tracking, *Nature*, *239*, 500–504, 1972.

Bergström, U., and G. Englund, Spatial scale, heterogeneity and functional responses, *Journal of Animal Ecology*, *73*, 487–493, 2004.

Bianco, G., P. Mariani, A. W. Visser, M. G. Mazzocchi, and S. Pigolotti, Analysis of self-overlap reveals trade-offs in plankton swimming trajectories, *Journal of The Royal Society Interface*, *11*, 20140164, 2014.

Bigelow, H. B., Plankton of the offshore waters of the gulf of maine: Us bur, *Fisheries Bull*, *40*, 509, 1926.

Blaire, D., and E. Dufresne, The matlab particle tracking code repository, `https://site.physics.georgetown.edu/matlab/index.htm`, 2008, accessed: 2017-01-24.

Blaxter, J., Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance, *Transactions of the American Fisheries Society*, *115*, 98–114, 1986.

Bochdansky, A. B., and D. Deibel, Consequences of model specification for the determination of gut evacuation rates: redefining the linear model, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 1032–1042, 2001.

Bousfield, E., The distribution and spawning seasons of barnacles on the atlantic coast of canada, *Bulletin of the National Museum of Canada*, *132*, 112–154, 1954.

Bousfield, E. L., *Ecological control of the occurrence of barnacles in the Miramichi estuary*, Dept. of Northern Affairs and National Resources, National Parks Branch, 1955.

Bradbury, I. R., and P. V. Snelgrove, Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 811–823, 2001.

Båmstedt, U., Trophodynamics of *Pleurobrachia pileus* (ctenophora, cydippida) and ctenophore summer occurrence off the norwegian north-west coast, *Sarsia*, *83*, 169–181, 1998.

Båmstedt, U., D. Gifford, X. Irigoien, A. Atkinson, and M. Roman, Feeding, in *ICES zooplankton methodology manual*, edited by R. Harris, P. Weibe, J. Lenz, H. Skjoldel, and M. Hundtly, Academic Press, 2000.

Branscomb, E. S., and K. Vedder, A description of the naupliar stages of the barnacles, balanus glandula darwin, balanus cariosus pallas, and balanus crena tus bruguière (cirripedia, thoracica), *Crustaceana*, *42*, 83–95, 1982.

Bromley, P. J., The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish, *Reviews in Fish Biology and Fisheries*, *4*, 36–66, 1994.

Bullard, S. G., N. L. Lindquist, and M. E. Hay, Susceptibility of invertebrate larvae to predators: how common are post-capture larval defenses?, *Marine Ecology Progress Series*, *191*, 153–161, 1999.

Buskey, E., Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food, *Marine Biology*, *79*, 165–175, 1984.

Buskey, E. J., and D. K. Stoecker, Locomotory patterns of the planktonic ciliate *Favella* sp.: adaptations for remaining within food patches, *Bulletin of Marine Science*, *43*, 783–796, 1988.

Chandrasekhar, S., Stochastic problems in physics and astronomy, *Reviews of modern physics*, *15*, 1, 1943.

Chandy, S. T., and C. H. Greene, Estimating the predatory impact of gelatinous zooplankton, *Limnology and oceanography*, *40*, 947–955, 1995.

Chesson, J., Measuring preference in selective predation, *Ecology*, *59*, 211–215, 1978.

Chia, F.-S., J. Buckland-Nicks, and C. M. Young, Locomotion of marine invertebrate larvae: a review, *Canadian Journal of Zoology*, *62*, 1205–1222, 1984.

Codling, E. A., M. J. Plank, and S. Benhamou, Random walk models in biology, *Journal of the Royal Society Interface*, *5*, 813–834, 2008.

Cohen, J. H., and R. B. Forward, Zooplankton diel vertical migration a review of proximate control, *Oceaongraphy and Marine Biology: An Annual Review*, *47*, 77–110, 2009.

Collins, F. C., and G. E. Kimball, Diffusion-controlled reaction rates, *Journal of colloid science*, *4*, 425–437, 1949.

Cowan, J., and E. D. Houde, Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in chesapeake bay, *Marine Ecology Progress Series*, *95*, 55–55, 1993.

Cowan, J. H., R. S. Birdsong, E. D. Houde, J. S. Priest, W. C. Sharp, and G. B. Mateja, Enclosure experiments on survival and growth of black drum eggs and larvae in lower chesapeake bay, *Estuaries and Coasts*, *15*, 392–402, 1992.

Cowan Jr, J. H., E. D. Houde, and K. A. Rose, Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment, *ICES Journal of Marine Science*, *53*, 23–37, 1996.

Cowen, R. K., K. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson, Connectivity of marine populations: open or closed?, *Science*, *287*, 857–859, 2000.

Crisp, D., The planktonic stages of the cirripedia balanus balanoides (l.) and balanus balanus (l.) from north temperate waters, *Crustaceana*, *3*, 207–221, 1962.

Crisp, D., and D. Ritz, Responses of cirripede larvae to light. i. experiments with white light, *Marine Biology*, *23*, 327–335, 1973.

Daan, N., A. Rijnsdorp, and G. Van Overbeeke, Predation by north sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*, *Transactions of the American Fisheries Society*, *114*, 499–506, 1985.

Daigle, R. M., and A. Metaxas, Vertical distribution of marine invertebrate larvae in response to thermal stratification in the laboratory, *Journal of experimental marine biology and ecology*, *409*, 89–98, 2011.

Daigle, R. M., and A. Metaxas, Modeling of the larval response of green sea urchins to thermal stratification using a random walk approach, *Journal of experimental marine biology and ecology*, *438*, 14–23, 2012.

Day, R., and L. McEdward, Aspects of the physiology and ecology of pelagic larvae of marine benthic invertebrates, in *Marine plankton life cycles*, edited by K. A. Steidinger and L. M. Walker, CRC Press, 1984.

de Lafontaine, Y., and W. Leggett, Predation by jellyfish on larval fish: an experimental evaluation employing *in situ* enclosures, *Canadian Journal of Fisheries and Aquatic Sciences*, *45*, 1173–1190, 1988.

de Lafontaine, Y. D., and W. C. Leggett, Effect of container size on estimates of mortality and predation rates in experiments with macrozooplankton and larval fish, *Canadian Journal of Fisheries and Aquatic Sciences*, *44*, 1534–1543, 1987.

DiBacco, C., H. L. Fuchs, J. Pineda, and K. Helfrich, Swimming behavior and velocities of barnacle cyprids in a downwelling flume, *Marine Ecology Progress Series*, *433*, 131–148, 2011.

Dunn, G. A., Characterising a kinesis response: time averaged measures of cell speed and directional persistence., *Agents and actions. Supplements*, *12*, 14, 1983.

Dur, G., S. Souissi, F. Schmitt, F.-G. Michalec, M.-S. Mahjoub, and J.-S. Hwang, Effects of animal density, volume, and the use of 2d/3d recording on behavioral studies of copepods, *Hydrobiologia*, *666*, 197–214, 2011.

Elliott, J., and W. Leggett, The effect of temperature on predation rates of a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*), *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1393–1402, 1996.

Evans, G. T., The encounter speed of moving predator and prey, *Journal of Plankton Research*, *11*, 415–417, 1989.

Fahay, M. P., Guide to the early stages of marine fishes occurring in the western north atlantic ocean, cape hatteras to the southern scotian shelf, *Journal of Northwest Atlantic Fishery Science*, *4*, 423, 1983.

Feigenbaum, D., and M. Reeve, Prey detection in the chaetognatha: response to a vibrating probe and experimental determination of attack distance in large aquaria, *Limnol. Oceanogr*, *22*, 1052–1058, 1977.

Fenchel, T., Suspended marine bacteria as a food source, in *Flows of energy and materials in marine ecosystems: Theory and practise*, edited by M. J. . R. Fasham, Plenum Press, 1984.

Fenchel, T., Marine plankton food chains, *Annual Review of Ecology and Systematics*, *19*, 19–38, 1988.

Fiksen, Ø., C. Jørgensen, T. Kristiansen, F. Vikebø, and G. Huse, Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal, 2007.

Forward, R., Depth regulation of larval marine decapod crustaceans: test of an hypothesis, *Marine Biology*, *102*, 195–201, 1989.

Forward, R. B., Behavioral responses of crustacean larvae to rates of temperature change, *The Biological Bulletin*, *178*, 195–204, 1990.

Forward, R. B., and R. A. Tankersley, Selective tidal-stream transport of marine animals, *Oceaongraphy and Marine Biology: An Annual Review*, *39*, 305–353, 2001.

Frank, K. T., Ecological significance of the ctenophore *Pleurobrachia pileus* off south-western nova scotia, *Canadian Journal of Fisheries and Aquatic Sciences*, *43*, 211–222, 1986.

Fraser, J., The ecology of the ctenophore *Pleurobrachia pileus* in scottish waters, *Journal du Conseil*, *33*, 149–168, 1970.

Fuchs, N. A., The coagulation of aerosols, in *The mechanics of aerosols*, edited by C. N. Davies, Pergamon, 1964.

Fuiman, L., The interplay of ontogeny and scaling in the interactions of fish larvae and their predators, *Journal of Fish Biology*, *45*, 55–79, 1994.

Fuiman, L. A., and J. C. Gamble, Predation by atlantic herring, sprat, and sandeels on herring larvae in large enclosures, *Marine Ecology Progress Series*, pp. 1–6, 1988.

Fuiman, L. A., and J. C. Gamble, Influence of experimental manipulations on predation of herring larvae by juvenile herring in large enclosures., in *ICES Marine Science Symposia. 1989.*, 1989.

Gaines, S. D., and J. Roughgarden, Fish in offshore kelp forests affect recruitment to intertidal barnacle populations., *Science(Washington)*, *235*, 479–480, 1987.

Gamble, J., and S. Hay, Predation by the scyphomedusan *Aurelia aurita* on herring larvae in large enclosures: Effects of predator size and prey starvation., in *ICES Marine Science Symposia. 1989.*, 1989.

Gardiner, W. C., Rate laws, in *Rates and mechanisms of chemical reactions*, edited by W. Kauzmann, Benjamin Inc, 1969.

Gentleman, W., A. Leising, B. Frost, S. Strom, and J. Murray, Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics, *Deep Sea Research Part II: Topical Studies in Oceanography*, *50*, 2847–2875, 2003.

Gentleman, W., P. Pepin, and S. Doucette, Estimating mortality: clarifying assumptions and sources of uncertainty in vertical methods, *Journal of Marine Systems*, *105*, 1–19, 2012.

Gerritsen, J., Adaptive response to encounter problems, in *Evolution and ecology of zooplankton communities*, edited by W. C. Kerfoot, University Press of New England, 1980.

Gerritsen, J., and J. R. Strickler, Encounter probabilities and community structure in zooplankton: a mathematical model, *Journal of the Fisheries Board of Canada*, *34*, 73–82, 1977.

Gibbons, M., and S. Painting, The effects and implications of container volume on clearance rates of the ambush entangling predator *Pleurobrachia pileus* (ctenophora: Tentaculata), *Journal of experimental marine biology and ecology*, *163*, 199–208, 1992.

Gorski, P. R., and S. I. Dodson, Free-swimming daphnia pulex can avoid following stokes' law, *Limnology and oceanography*, *41*, 1815–1821, 1996.

Govoni, J. J., Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years, *Scientia marina*, *69*, 125–137, 2005.

Greene, C. H., Selective predation in freshwater zooplankton communities, *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, *68*, 297–315, 1983.

Greene, C. H., M. R. Landry, and B. C. Monger, Foraging behavior and prey selection by the ambush entangling predator pleurobrachia bachei, *Ecology*, *67*, 1493–1501, 1986.

Gregory, D., B. Petrie, F. Jordan, and P. Langille, Oceanographic, geographic, and hydrological parameters of scotia-fundy and southern gulf of st lawrence inlets, *Canadian Technical Report of Hydrography and Ocean Sciences*, 1993.

Grosberg, R. K., Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults, *Ecology*, pp. 894–899, 1982.

Hansson, L. J., A method for *in situ* estimation of prey selectivity and predation rate in large plankton, exemplified with the jellyfish *Aurelia aurita* (l.), *Journal of Experimental Marine Biology and Ecology*, *328*, 113–126, 2006.

Hansson, L. J., and T. Kiørboe, Prey-specific encounter rates and handling efficiencies as causes of prey selectivity in ambush-feeding hydromedusae, *Limnology and oceanography*, *51*, 1849–1858, 2006.

Hansson, L. J., O. Moeslund, T. Kiørboe, and H. U. Riisgård, Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (limfjorden, denmark), *Marine Ecology Progress Series*, *304*, 117–131, 2005.

Harris, R. P., M. R. Reeve, G. D. Grice, G. T. Evans, V. R. Gibson, J. R. Beers, and B. K. Sullivan, Trophic interactions and production processes in natural zooplankton communities in enclosed water columns, in *Marine mesocosms*, edited by G. G. D. and M. R. Reeve, pp. 353–387, Springer, 1982.

Harris, S., Steady absorption of brownian particles by a sphere, *The Journal of Chemical Physics*, *77*, 934–938, 1982.

Heath, M., Field investigations of the early life stages of marine fish, *Advances in marine biology*, *28*, 1–174, 1992.

Helbig, J., and P. Pepin, Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates. ii. application to simulated and field data, *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 2206–2220, 1998.

Henriksen, C. I., E. Saiz, A. Calbet, and B. W. Hansen, Feeding activity and swimming patterns of *Acartia grani* and *Oithona davisae* nauplii in the presence of motile and non-motile prey, *Marine Ecology Progress Series*, *331*, 119–129, 2007.

Hidu, H., and H. H. Haskin, Swimming speeds of oyster larvae crassostrea virginica in different salinities and temperatures, *Estuaries and Coasts*, *1*, 252–255, 1978.

Hirche, H.-J., Temperature and plankton, *Marine biology*, *94*, 347–356, 1987.

Hirota, J., Quantitative natural history of pleurobrachia bachei in la jolla bight, *Fish. Bull*, *72*, 295–335, 1974.

Holling, C. S., The components of predation as revealed by a study of small-mammal predation of the european pine sawfly, *The Canadian Entomologist*, *91*, 293–320, 1959a.

Holling, C. S., Some characteristics of simple types of predation and parasitism, *The Canadian Entomologist*, *91*, 385–398, 1959b.

Houde, E. D., Mortality, in *Fishery science: the unique contributions of early life stages*, edited by A. Fuiman and R. G. Wener, Blackwell Science Ltd, 2002.

Hughes, I., and T. Hase, *Measurements and their uncertainties: a practical guide to modern error analysis*, Oxford University Press, 2010.

Hunter, J., and C. Kimbrell, Egg cannibalism in the northern anchovy, engraulis mordax, *Fishery Bulletin*, *78*, 811–816, 1980.

Hutchinson, J., and P. M. Waser, Use, misuse and extensions of ideal gas models of animal encounter, *Biological Reviews*, *82*, 335–359, 2007.

Ives, A. R., S. S. Schooler, V. J. Jagar, S. E. Knuteson, M. Grbic, and W. H. Settle, Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*, *The American Naturalist*, *154*, 652–673, 1999.

Ivlev, V. S., *Experimental ecology of the feeding of fishes*, London, 1964.

Jaspers, C., J. Titelman, L. J. Hansson, M. Haraldsson, and C. R. Ditlefsen, The invasive ctenophore mnemiopsis leidyi poses no direct threat to baltic cod eggs and larva, *Limnology and Oceanography*, *56*, 431–439, 2011.

Jobling, M., Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish, *Journal of fish biology*, *19*, 245–257, 1981.

Johnson, K. B., and A. L. Shanks, The importance of prey densities and background plankton in studies of predation on invertebrate larvae, *Marine Ecology Progress Series*, *158*, 293–296, 1997.

Johnson, K. B., and A. L. Shanks, Low rates of predation on planktonic marine invertebrate larvae, *Marine Ecology Progress Series*, *248*, 125–139, 2003.

Johnson, W. S., and D. M. Allen, *Zooplankton of the Atlantic and Gulf coasts: a guide to their identification and ecology*, JHU Press, 2012.

Karp-Boss, L., E. Boss, P. Jumars, et al., Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion, *Oceanography and Marine Biology*, *34*, 71–108, 1996.

Kimmerer, W. J., Selective predation and its impact on prey of *Sagitta enflata* (chaetognatha), *Mar. Ecol. Prog. Ser*, *15*, 55–62, 1984.

Kingsford, M. J., J. M. Leis, A. Shanks, K. C. Lindeman, S. G. Morgan, and J. Pineda, Sensory environments, larval abilities and local self-recruitment, *Bulletin of Marine Science*, *70*, 309–340, 2002.

Kiørboe, T., Small-scale turbulence, marine snow formation, and planktivorous feeding, *Scientia Marina*, *61*, 141–158, 1997.

Kiørboe, T., *A mechanistic approach to plankton ecology*, Princeton University Press, 2008.

Kiørboe, T., How zooplankton feed: mechanisms, traits and trade-offs, *Biological Reviews*, *86*, 311–339, 2011.

Kiørboe, T., and E. Bagøien, Patterns and mate encounter rates in planktonic copepods, *Limnology and Oceanography*, *50*, 1999–2007, 2005.

Kiørboe, T., and B. MacKenzie, Turbulence-enhanced prey encounter rates in larval fish: effects of spatial scale, larval behaviour and size, *Journal of Plankton Research*, *17*, 2319–2331, 1995.

Kiørboe, T., F. Møhlenberg, and K. Hamburger, Bioenergetics of the planktonic copepod textitAcartia tonsa: relation between feeding, egg production and respiration, and composition of specific dynamic action, *Marine Ecology Progress Series*, *26*, 85–97, 1985.

Kiørboe, T., H.-P. Grossart, H. Ploug, K. Tang, and B. Auer, Particle-associated flagellates: swimming patterns, colonization rates, and grazing on attached bacteria, *Aquatic Microbial Ecology*, *35*, 141–152, 2004.

Koch, A. L., The adaptive responses of escherichia coli to a feast and famine existence, *Advances in microbial physiology*, *6*, 147–217, 1971.

Kuipers, B. R., U. Gaedke, L. Enserink, and H. Witte, Effect of ctenophore predation on mesozooplankton during a spring outburst of *Pleurobrachia pileus*, *Netherlands Journal of Sea Research*, *26*, 111–124, 1990.

Lamare, M. D., and M. F. Barker, *In situ* estimates of larval development and mortality in the new zealand sea urchin evechinus chloroticus (echinodermata: Echinoidea), *Marine Ecology Progress Series*, *180*, 197–211, 1999.

Lang, W., Cirripedia: balanomorph nauplii of the nw atlantic shores, *Fiches dIdentification du Zooplancton*, *163*, 1–6, 1980.

Lang, W. H., and A. Ackenhusen-Johns, Seasonal species composition of barnacle larvae (cirripedia: Thoracica) in rhode island waters, 1977–1978, *Journal of Plankton Research*, *3*, 567–575, 1981.

Lang, W. H., M. Marcy, P. J. Clem, D. C. Miller, and M. R. Rodelli, The comparative photobehavior of laboratory-hatched and plankton-caught balanus improvisus (darwin) nauplii and the effects of 24-hour starvation, *Journal of Experimental Marine Biology and Ecology*, *42*, 201–212, 1980.

Larsen, P. S., and H. U. Riisgård, Viscosity and not biological mechanisms often controls the effects of temperature on ciliary activity and swimming velocity of small aquatic organisms, *Journal of Experimental Marine Biology and Ecology*, *381*, 67–73, 2009.

Larsen, P. S., C. V. Madsen, and H. U. Riisgård, Effect of temperature and viscosity on swimming velocity of the copepod acartia tonsa, brine shrimp artemia salina and rotifer brachionus plicatilis, *Aquatic Biology*, *4*, 47–54, 2008.

Larson, R., Daily ration and predation by medusae and ctenophores in saanich inlet, bc, canada, *Netherlands Journal of Sea Research*, *21*, 35–44, 1987.

Lebour, M. V., The food of plankton organisms, *Journal of the Marine Biological Association of the United Kingdom (New Series)*, *12*, 644–677, 1922.

Levandowsky, M., J. Klafter, and B. White, Feeding and swimming behavior in grazing microzooplankton, *The Journal of protozoology*, *35*, 243–246, 1988.

Lima, S. L., and L. M. Dill, Behavioral decisions made under the risk of predation: a review and prospectus, *Canadian Journal of Zoology*, *68*, 619–640, 1990.

Lincoln, R., Observations of the effects of changes in hydrostatic pressure and illumination on the behaviour of some planktonic crustaceans, *J. exp. Biol*, *54*, 677–688, 1971.

Lindquist, N., and M. E. Hay, Palatability and chemical defense of marine invertebrate larvae, *Ecological Monographs*, *66*, 431–450, 1996.

Lindström, M., and W. Fortelius, Swimming behaviour in monoporeia affinis (crustacea: Amphipoda)dependence on temperature and population density, *Journal of experimental marine biology and ecology*, *256*, 73–83, 2001.

Litchman, E., M. D. Ohman, and T. Kiørboe, Trait-based approaches to zooplankton communities, *Journal of Plankton Research*, *35*, 473–484, 2013.

Litvak, M. K., and W. C. Leggett, Age and size-selective predation on larval fishes: The bigger-is-better hypothesis revisited., *Marine ecology progress series. Oldendorf*, *81*, 13–24, 1992.

Lovely, P. S., and F. Dahlquist, Statistical measures of bacterial motility and chemotaxis, *Journal of theoretical biology*, *50*, 477–496, 1975.

Lucas, M., G. Walker, D. Holland, and D. Crisp, An energy budget for the free-swimming and metamorphosing larvae of balanus balanoides (crustacea: Cirripedia), *Marine Biology*, *55*, 221–229, 1979.

MacKenzie, B. R., T. J. Miller, S. Cyr, and W. C. Leggett, Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates, *Limnology and Oceanography*, *39*, 1790–1799, 1994.

Marshall, S. M., A. Nicholls, and A. Orr, On the growth and feeding of the larval and post-larval stages of the clyde herring, *Journal of the Marine Biological Association of the United Kingdom*, *22*, 245–267, 1937.

Martin, L. E., Limitations on the use of impermeable mesocosms for ecological experiments involving *Aurelia* sp.(scyphozoa: Semaeostomeae), *Journal of plankton research*, *23*, 1–10, 2001.

Matsakis, S., and R. J. Conover, Abundance and feeding of medusae and their potential impact as predators on other zooplankton in bedford basin (nova scotia, canada) during spring, *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1419–1430, 1991.

Matsuno, K., A. Yamaguchi, and I. Imai, Biomass size spectra of mesozooplankton in the chukchi sea during the summers of 1991/1992 and 2007/2008: an analysis using optical plankton counter data, *ICES Journal of Marine Science: Journal du Conseil*, p. fss119, 2012.

Maxwell, J. C., Illustrations of the dynamical theory of gases.part i. on the motions and collisions of perfectly elastic spheres, *Philosophical Magazine*, *19*, 19–32, 1860.

McDonald, K., Patterns in early embryonic motility: effects of size and environmental temperature on vertical velocities of sinking and swimming echinoid blastulae, *The Biological Bulletin*, *207*, 93–102, 2004.

Menden-Deuer, S., and D. Grünbaum, Individual foraging behaviors and population distributions of a planktonic predator aggregating to phytoplankton thin layers, *Limnology and Oceanography*, *51*, 109–116, 2006.

Menden-Deuer, S., and T. Kiørboe, Small bugs with a big impact: linking plankton ecology with ecosystem processes, *Journal of Plankton Research*, 2016.

Metaxas, A., and M. Saunders, Quantifying the bio- components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls, *The Biological Bulletin*, *216*, 257–272, 2009.

Miller, T. J., Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations, *Marine Ecology Progress Series*, *347*, 127–138, 2007.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall, Larval size and recruitment mechanisms in fishes: toward a conceptual framework, *Canadian Journal of Fisheries and Aquatic Sciences*, *45*, 1657–1670, 1988.

Milne, W., and S. Corey, Distributional patterns of the ctenophores *Pleurobrachia pileus* and *Beroe cucumis* in the bay of fundy region, canada, *Canadian journal of zoology*, *64*, 2639–2644, 1986.

Moison, M., F. G. Schmitt, and S. Souissi, Effect of temperature on temora longicornis swimming behaviour: Illustration of seasonal effects in a temperate ecosystem, *Aquatic Biology*, *16*, 149–162, 2012.

Morgan, S. G., Adaptive significance of spination in estuarine crab zoeae, *Ecology*, *70*, 464–482, 1989.

Morgan, S. G., Life and death in the plankton: Larval mortality and adaptation, in *Ecology of Marine Invertebrate Larvae*, edited by L. McEdwards, CRC Press, 1995.

Mullin, M. M., Differential predation by the carnivorous marine copepod, *Tortanus discaudatus*, *Limnology and Oceanography*, *24*, 774–777, 1979.

Nachman, G., A functional response model of a predator population foraging in a patchy habitat, *Journal of Animal Ecology*, *75*, 948–958, 2006.

Navarrete, S. A., and E. A. Wieters, Variation in barnacle recruitment over small scales: larval predation by adults and maintenance of community pattern, *Journal of experimental marine biology and ecology*, *253*, 131–148, 2000.

Neuheimer, A., W. Gentleman, P. Pepin, and E. Head, Explaining regional variability in copepod recruitment: Implications for a changing climate, *Progress in Oceanography*, *87*, 94–105, 2010.

Neumann, V., M. Schaber, M. Eero, U. Böttcher, and F. W. Köster, Quantifying predation on baltic cod early life stages, *Canadian Journal of Fisheries and Aquatic Sciences*, pp. 1–10, 2016.

Ohman, M., Behavioral responses of zooplankton to predation, *Bulletin of Marine Science*, *43*, 530–550, 1988.

Olson, R. R., and R. McPherson, Potential vs. realized larval dispersal: fish predation on larvae of the ascidian lissoclinum patella (gottschaldt), *Journal of Experimental Marine Biology and Ecology*, *110*, 245–256, 1987.

Ouellet, P., and J.-P. Allard, Vertical distribution and behaviour of shrimp *Pandalus borealis* larval stages in thermally stratified water columns: laboratory experiment and field observations, *Fisheries Oceanography*, *15*, 373–389, 2006.

Paradis, A., P. Pepin, and J. Brown, Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator, *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 1226–1235, 1996.

Paranjape, M., and R. . Conover, Zooplankton of st. margarets bay 1968 to 1971, *Fisheries Research Board of Cananada Technical Report*, *401*, 1–39, 1973.

Pasciak, W. J., and J. Gavis, Transport limitation of nutrient uptake in phytoplankton, *Limnology and Oceanography*, *19*, 881–888, 1974.

Pennington, J. T., The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning, *Biological Bulletin*, *169*, 417–430, 1985.

Pennington, J. T., S. S. Rumrill, and F.-S. Chia, Stage-specific predation upon embryos and larvae of the pacific sand dollar, dendraster excentricus, by 11 species of common zooplanktonic predators, *Bulletin of Marine Science*, *39*, 234–240, 1986.

Pennington, M., Estimating the average food consumption by fish in the field from stomach contents data, *Dana*, *5*, 81–86, 1981.

Pepin, P., Influence of alternative prey abundance on pelagic fish predation of larval fish: a model, *Canadian Journal of Fisheries and Aquatic Sciences*, *44*, 222–227, 1987.

Pepin, P., Estimating the encounter rate of atlantic capelin (*Mallotus villosus*) with fish eggs, based on stomach content analysis, *Fishery Bulletin*, *104*, 204–214, 2006.

Pepin, P., T. Shears, and Y. De Lafontaine, Significance of body size to the interaction between a larval fish (mallotus villosus) and a vertebrate predator (gasterosteus aculeatus), *Marine Ecology Progress Series*, pp. 1–12, 1992.

Pepin, P., J. Dower, J. Helbig, and W. Leggett, Estimating the relative roles of dispersion and predation in generating regional differences in mortality rates of larval radiated shanny (ulvaria subbifurcata), *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 105–114, 2002.

Pineda, J., D. Riebensahm, and D. Medeiros-Bergen, Semibalanus balanoides in winter and spring: larval concentration, settlement, and substrate occupancy, *Marine Biology*, *140*, 789–800, 2002.

Podolsky, R., and R. Emlet, Separating the effects of temperature and viscosity on swimming and water movement by sand dollar larvae (dendraster excentricus), *Journal of Experimental Biology*, *176*, 207–222, 1993.

Purcell, J. E., Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae, *Limnol. Oceanogr*, *26*, 424–432, 1981.

Purcell, J. E., Predation on fish larvae by*Physalia physalis*, the portuguese man of war., *Marine ecology progress series. Oldendorf*, *19*, 189–191, 1984.

Purcell, J. E., Predation on fish larvae and eggs by the hydromedusa aequorea victoria at a herring spawning ground in british columbia, *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 1415–1427, 1989.

Purcell, J. E., and J. J. Grover, Predation and food limitation as causes of mortality in larval herring at a spawning ground in british columbia, 1990.

Purcell, J. E., and C. E. Mills, The correlation between nemato cyst types and diets in pelagic hydrozoa, in *The biology of nematocysts*, edited by D. A. Hessinger and H. M. Lenhoff, Academic Press, 1988.

Purcell, J. E., F. P. Cresswell, D. G. Cargo, and V. S. Kennedy, Differential ingestion and digestion of bivalve larvae by the scyphozoan chrysaora quinquecirrha and the ctenophore mnemiopsis leidyi, *The Biological Bulletin*, *180*, 103–111, 1991.

Purcell, J. E., D. A. Nemazie, S. E. Dorsey, E. D. Houde, and J. C. Gamble, Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in chesapeake bay, *Marine Ecology Progress Series*, pp. 47–58, 1994.

Purcell, J. E., U. Tilves, V. L. Fuentes, G. Milisenda, A. Olariaga, and A. Sabatés, Digestion times and predation potentials of *Pelagia noctiluca* eating fish larvae and copepods in the nw mediterranean sea, *Marine Ecology Progress Series*, *510*, 201–213, 2014.

Queiroga, H., and J. Blanton, Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae, *Advances in marine biology*, *47*, 107–214, 2004.

Reeve, M., and M. Walter, Nutritional ecology of ctenophoresa review of recent research, *Advances in marine biology*, *15*, 249–287, 1979.

Rice, A., Observations on the effects of changes of hydrostatic pressure on the behaviour of some marine animals, *Journal of the Marine Biological Association of the United Kingdom*, *44*, 163–175, 1964.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis, Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model, *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 133–142, 1993.

Rothschild, B., and T. Osborn, Small-scale turbulence and plankton contact rates, *Journal of Plankton Research*, *10*, 465–474, 1988.

Rowe, M. D., Some aspects of the feeding behavior of the ctenophore *Pleurobrachia pileus*, Ph.D. thesis, University of Hawaii, 1971.

Rumrill, S. S., Natural mortality of marine invertebrate larvae, *Ophelia*, *32*, 163–198, 1990.

Saito, H., and T. Kiørboe, Feeding rates in the chaetognath sagitta elegans: effects of prey size, prey swimming behaviour and small-scale turbulence, *Journal of Plankton Research*, *23*, 1385–1398, 2001.

Saiz, E., and T. Kiørboe, Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments, *Marine Ecology-Progress Series*, *122*, 147–158, 1995.

Saiz, E., A. Calbet, and E. Broglio, Effects of small-scale turbulence on copepods: The case of *Oithona davisae*, *Limnology and Oceanography*, *48*, 1304–1311, 2003.

Sameoto, D., Annual life cycle and production of the chaetognath sagitta elegans in bedford basin, nova scotia, *Journal of the Fisheries Board of Canada*, *30*, 333–344, 1973.

Santander, H., J. Alheit, A. MacCall, and A. Alamo, Egg mortality of the peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*), *FAO Fishery and Aquaculture Report*, *3*, 1011–1025, 1983.

Schuech, R., and S. Menden-Deuer, Going ballistic in the plankton: Anisotropic swimming behavior of marine protists, *Limnology and Oceanography: Fluids and Environments*, *4*, 1–16, 2014.

Shanks, A. L., and W. G. Wright, Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles, *Journal of Experimental Marine Biology and Ecology*, *114*, 1–13, 1987.

Short, J., A. Metaxas, and R. M. Daigle, Predation of larval benthic invertebrates in st georges bay, nova scotia, *Journal of the Marine Biological Association of the United Kingdom*, *93*, 591–599, 2013.

Singarajah, K., Escape reactions of zooplankton: the avoidance of a pursuing siphon tube, *Journal of Experimental Marine Biology and Ecology*, *3*, 171–178, 1969.

Smoluchowski, M., Drei vortrage uber diffusion. brownsche bewegung und koagulation von kolloidteilchen, *Zeitschrift für Physik*, *17*, 557–585, 1916.

Sorochan, K. A., and A. Metaxas, Low predation rates on the larvae of three species of barnacles by the ctenophore *Pleurobrachia pileus*, *Marine Ecology Progress Series*, *541*, 105–122, 2015.

Sorochan, K. A., W. C. Gentleman, and A. Metaxas, Modelling rates of random search over the transition from diffusive to ballistic movement of plankton, *Journal of Plankton Research*, p. https://doi.org/10.1093/plankt/fbx034, 2017.

Stickney, A. P., and H. C. Perkins, Observations on the food of the larvae of the northern shrimp, pandal us borealis kroyer (decapoda, caridea), *Crustaceana*, *40*, 36–49, 1981.

Strathmann, R. R., Feeding and nonfeeding larval development and life-history evolution in marine invertebrates, *Annual review of ecology and systematics*, *16*, 339–361, 1985.

Sulkin, S., W. Van Heukelem, P. Kelly, and L. Van Heukelem, The behavioral basis of larval recruitment in the crab callinectes sapidus rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis, *The Biological Bulletin*, *159*, 402–417, 1980.

Sullivan, B., and M. Reeve, Comparison of estimates of the predatory impact of ctenophores by two independent techniques, *Marine Biology*, *68*, 61–65, 1982.

Svensen, C., and T. Kiørboe, Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues, *Journal of Plankton Research*, *22*, 1155–1166, 2000.

Svetlichny, L., E. Hubareva, and M. Isinibilir, Comparative trends in respiration rates, sinking and swimming speeds of copepods pseudocalanus elongatus and acartia clausi with comments on the cost of brooding strategy, *Journal of Experimental Marine Biology and Ecology*, *488*, 24–31, 2017.

Szeinfeld, E. V., Cannibalism and intraguild predation in clupeoids., *Marine ecology progress series. Oldendorf*, *79*, 17–26, 1991.

Taggart, C., and W. Leggett, Short-term mortality in post-emergent larval capelin mallotus villosus. i. analysis of multiple *in situ* estimates, *Marine Ecology Progress Series*, pp. 205–217, 1987.

Taggart, C. T., and K. F. Frank, Perspectives on larval fish biology ecology and recruitment processes: probing the scales of relationships, in *Patterns, processes, and yields of large marine ecosystems*, edited by K. Sherman and L. M. Alexander, AAAS selected Symposium Series, 1995.

Tapia, F. J., and J. Pineda, Stage-specific distribution of barnacle larvae in nearshore waters: potential for limited dispersal and high mortality rates, 2007.

Tapia, F. J., C. DiBacco, J. Jarrett, and J. Pineda, Vertical distribution of barnacle larvae at a fixed nearshore station in southern california: Stage-specific and diel patterns, *Estuarine, Coastal and Shelf Science*, *86*, 265–270, 2010.

Taylor, G. I., Diffusion by continuous movements, *Proceedings of the London Mathematical Society*, *2*, 196–212, 1922.

Theilacker, G. H., Euphausiid predation on larval anchovy at two contrasting sites off california determined with an elispot immunoassay, in *Immunochemical approaches to coastal, estuarine and oceanographic questions*, edited by M. Yentsch, F. C. Mague, and P. K. Horan, Springer, 1995.

Thorson, G., Reproductive and larval ecology of marine bottom invertebrates, *Biological reviews*, *25*, 1–45, 1950.

Titelman, J., and T. Kiørboe, Motility of copepod nauplii and implications for food encounter, *Marine Ecology Progress Series*, *247*, 123–135, 2003.

Tönnesson, K., and P. Tiselius, Diet of the chaetognaths sagitta setosa ands. elegans in relation to prey abundance andvertical distribution, *Marine Ecology Progress Series*, *289*, 177–190, 2005.

Townsend, D. W., Comparison of inshore zooplankton and ichthyoplankton populations of the gulf of maine, *Marine ecology progress series. Oldendorf*, *15*, 79–90, 1984.

Underwood, A., and P. Fairweather, Supply-side ecology and benthic marine assemblages, *Trends in Ecology & Evolution*, *4*, 16–20, 1989.

Underwood, A. J., *Experiments in ecology: their logical design and interpretation using analysis of variance*, Cambridge University Press, 1997.

Uye, S.-i., and Y. Kayano, Predatory feeding behavior of *Tortanus* (copepoda: Calanoida): life-stage differences and the predation impact on small planktonic crustaceans, *Journal of Crustacean Biology*, *14*, 473–473, 1994.

Vaughn, D., and J. D. Allen, The peril of the plankton, *Integrative and Comparative Biology*, *50*, 552–570, 2010.

Verity, P. G., Feeding in planktonic protozoans: Evidence for non-random acquisition of prey, *The Journal of protozoology*, *38*, 69–76, 1991.

Vinyard, G. L., and W. J. Obrien, Effects of light and turbidity on the reactive distance of bluegill (lepomis macrochirus), *Journal of the Fisheries Board of Canada*, *33*, 2845–2849, 1976.

Visser, A. W., Motility of zooplankton: fitness, foraging and predation, *Journal of Plankton research*, *29*, 447–461, 2007.

Visser, A. W., and T. Kiørboe, Plankton motility patterns and encounter rates, *Oecologia*, *148*, 538–546, 2006.

Visser, A. W., and U. H. Thygesen, Random motility of plankton: diffusive and aggregative contributions, *Journal of plankton research*, *25*, 1157–1168, 2003.

Vlymen, W. J., A mathematical model of the relationship between larval anchovy (engraulis mordax) growth, prey microdistribution, and larval behavior, *Environmental Biology of Fishes*, *2*, 211–233, 1977.

Walker, G., Swimming speeds of the larval stages of the parasitic barnacle, heterosaccus lunatus (crustacea: Cirripedia: Rhizocephala), *Journal of the Marine Biological Association of the UK*, *84*, 737–742, 2004.

Walker, G., A. Yule, and J. Nott, Structure and function in balanomorph larvae, in *Barnacle Biology*, edited by A. J. Southward, Balkema: Rotterdam, 1987.

Walley, L. J., and E. Rees, Studies on the larval structure and metamorphosis of balanus balanoides (l.), *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *256*, 237–280, 1969.

White, J. W., S. G. Morgan, and J. L. Fisher, Planktonic larval mortality rates are lower than widely expected, *Ecology*, *95*, 3344–3353, 2014.

Woodson, C., D. Webster, M. Weissburg, and J. Yen, Response of copepods to physical gradients associated with structure in the ocean, *Limnology and Oceanography*, *50*, 1552–1564, 2005.

Young, C. M., and F. S. Chia, Abundance and distribution of pelagic larvae as influenced by predation, behaviour, and hydrodynamic factors, in *Reproduction of Marine Invertebrates*, edited by A. G. Giese and J. S. Pearse, Academic Press, 1987.

Yule, A., The effect of temperature on the swimming activity of barnacle nauplii, *Marine biology letters*, *5*, 1–11, 1984.

Zar, J., *Biostatistics*, Princeton hall. London, 1984.

Zar, J., *Biostatistical analysis*, Pearson Education India, 1999.