Use of a growth model to estimate size at age in the temperate sea cucumber *Australostichopus mollis*

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Abstract

Exposure to unstable and dynamic habitats influences sea cucumber life history characteristics such as growth and survival. Consequently, size is affected by the habitat a species has adapted to over time. Size and seasonal trends in growth and mortality of a population of *Australostichopus mollis* reflect this. Typically, *A. mollis* population growth halted in the winter months of May, June, July, and resumed through late spring, summer and early autumn. A growth model can be used to estimate size at age, provided cohorts through time are identified and the sample is representative of the population. Although the population appeared unimodal due to the inability to identify juvenile cohorts, the Pauly seasonal modification of the von Bertalanffy growth equation was applied and calculated asymptotic population weight at 130 g after three years. K, the rate at which asymptotic weight was approached, was 1.37 yr^{-1}. Age slicing identified two age groups in the population, year 0 and year 1. Weight at the start of year 0 was 17 g, increasing to 100 g in the second year of growth (year 1). In addition, mortality had a strong influence on population dynamics, with instantaneous natural population mortality (M) of 0.58 and a maximum total population mortality rate (Z) of 1.5 yr^{-1}. For sea cucumbers such as *A. mollis* that exist in ruderal, unstable, and dynamic environments, growth rate is high but mean adult size is reduced while mortality is usually high but variable. Parameter estimates reflected those for other sea cucumber species with similar life history traits. Provided juvenile cohorts can be identified, in the future the growth model would be useful in determining further the population parameters of *A. mollis*.

Introduction

Traditionally, changes in weight and associated reproductive indices, variation in mean population weight and maximum adult weight, and in particular the determination of size at first reproduction or sexual maturity, have been used to describe growth characteristics of sea cucumbers (Cameron and Fankboner 1985, 1989; Conand 1988, 1989, 1993; Conand et al. 1998; Raj 1998; Ramofafia et al. 2000; Sewell 1990, 1992; Sewell and Bergquist 1990; Toral-Granda and Martinez 2008; Uthicke 1997). These growth characteristics are used to understand in an ecological context the expression of life history traits in both juveniles and adults of a population. For example, the growth of caged juveniles of *Australostichopus mollis* has been followed over a nine-month period at various locations and growth compared with sediment characteristics, food availability and habitat (Slater and Jeffs 2010). Such growth characteristics can be compared within and between species and related to ecological observations on habitat adaptation. In particular, how low stress and high disturbance habitats impact on population growth and survival (Carlow 1984; Lawrence and Bazhin 1998; Lawrence and Herrera 2000). Such habitat adaptation is related to the tradeoff between growth and survival.

Previously, the von Bertalanffy growth equation and its variants (Basson et al. 1988; Pauly 1987; Hoenig and Hanumara 1982) have also been used to determine population growth and mortality parameters and to describe growth characteristics for some species of sea cucumbers. These population parameters can be used to further evaluate population dynamics. Asymptotic population weight (L_∞) and the Shephard method (Shephard 1987a) for estimation of the growth coefficient (K), the rate at which the population approaches asymptotic population weight, are estimated. The parameter t_0 is also computed, representing a point in time at which animals are essentially "born". The Pauly model for seasonal growth is also used where strong seasonal growth is suspected (Pauly 1987). The von Bertalanffy constants are then used to determine instantaneous natural mortality (M) along with total mortality rate (Z), which is estimated from a regression capture curve. Such estimates of population growth and mortality have been quantified for the sea cucumbers *Thelenota ananas*, *Stichopus chloronotus* and *Isostichopus fuscus* and *Holothuria floridana* (Conand 1988; Ebert 1978; Fuente-Betancourt et al. 2001; Hearn et al. 2005; Reyes-Bonilla and Herrera-Perezrul 2003).

The rate at which growth (K) approaches asymptotic population weight has been determined for

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H. floridana (Fuente-Betancourt et al. 2001) and for *T. ananas* and *S. chloronotus* (Conand 1988). High values of K are associated with rates of growth that approach asymptotic population weight quickly, usually greater than 1.0 yr^{-1} (Sparre et al. 1989). Typically, in populations of sea cucumbers with high values of K, total mortality rates are often greater than 0.5 yr^{-1} but may vary. Total mortality rate (Z) and natural instantaneous mortality (M), have been estimated for populations of *I. fuscus* (Hearn et al. 2005; Herrera-Perezrul and Reyes-Bonilla 2008; Herrera-Perezrul et al. 1999; Toral-Granda and Martinez 2007; Reyes-Bonilla and Herrera-Perezrul 2003). The mortality rate has also been determined for *H. floridana* (Fuente-Bentancourt et al. 2001). These population parameters can be used to further understand exogenous influences on growth characteristics such as size at 1 year, size at first reproduction, adult size and life history characteristics.

The sea cucumber *Australostichopus mollis* is distributed widely around New Zealand, and occupies a range of habitats (Mladenov and Campbell 1996; Shears and Babcock 2007). It is also found in Australia on the southern coast of New South Wales, Victoria and Western Australia (Sewell 1990). It can be found in a wide range of habitats and depths, from shallow inshore waters on rocky and sandy substrates to mud seafloors at depths exceeding 100 m (Dawbin 1949). The basic ecology, reproduction and larval development and juvenile and adult nutrition of *A. mollis* have been described (Archer 1996 Morgan 2008a, 2008b, 2009a, 2009b; Raj 1998; Sewell 1990, 1992; Sewell and Bergquist 1990; Slater and Carton 2007; Slater and Jeffs 2010). *A. mollis* is typically 13–25 cm in length and has a unimodal, size-frequency distribution and the viscera index maintains an approximate uniform value throughout the year (Sewell 1990). The contribution of gonad-to-weight fluctuation is minimal (Archer 1998; Sewell 1990) but seasonal diapause and food availability may contribute to some variation in body-wall weight over time (Sewell 1990; Slater and Jeffs 2010). This has also been found for *Parastichopus californicus*, which remains in diapause until conditions improve (Silva et al. 1986) and for *Holothuria theeli* (Sonnenholzer 2003).

The objective of the present study was to record changes in the distribution of weight of *A. mollis* over a year for an *in situ* population and model growth to determine size at age. Model parameters are then discussed and compared in terms of sea cucumber growth, life history characteristics and habitat adaptation. The present study is constrained by a number of factors, including the unimodal, size-frequency distribution of *A. mollis*. The study is conducted at one site and precludes following a cohort of juveniles through time due to not finding them in any significant numbers. Growth and mortality parameters were determined based on the "adult" population.

Materials and methods

Collection and sampling

A population of *A. mollis* was sampled once every two months on a subtidal rocky reef on the northeast coast of New Zealand at Ti Point for one year. Ti Point Peninsula (36° 19′24 S 174° 48′04 E) is 90 km north of Auckland and 5 km south of Leigh Marine Reserve in northeastern New Zealand (Sewell 1990). Sampling was carried out once every two months because a pilot study where *A. mollis* was collected once a month for seven months indicated that sampling frequency at short intervals confounded results. The headland of Ti Point is adjacent to the entrance to Whangateau Harbour. Its benthic habitat consists of a rocky subtidal reef made up of rocks and boulders, including large stands of *Ecklonia radiata* kelp, leveling out to a sand bottom at approximately 10 m. It is a site at the northern end of the Hauraki Gulf. Winds are generally from the southwest although occasional strong winds are experienced from the north and southeast.

Animals were always collected from the same location and within a 50 × 50 m^2 area using large catch bags. The sampled weight-frequency distributions were also representative of the population at Ti Point (Archer 1998; Morgan 2009a; Sewell 1990). A small vessel was used to access the survey site. Sampling was carried out on days with relatively calm sea conditions. Sea cucumbers were collected using scuba, and were placed in catch bags, taken to the surface, and placed in 20-L tubs of seawater on the vessel. The vessel was relocated to a sheltered area inside the adjacent Whangateau Harbour entrance, and while at anchor the sea cucumbers were weighed to the nearest 5 g. Weight was recorded for each individual collected and the animals were returned (by scuba) together to the site they were gathered from and placed back on the sea bed.

Growth

Data were formatted for modeling, and dates converted to proportions of a 365 day year. Starting with the first sampling date of 14 October, this was divided by 365. For each subsequent sampling date the previous number of days were added and the total divided by 365. For each sampling date, sea cucumbers counts were grouped in 20-g size intervals and Length Frequency Distribution Analysis (LFDA) Version 5 — see www.fmsp.org.uk — was used to analyse the dataset.

The von Bertalanffy model is the simplest of the LFDA growth models and requires three parameters to be estimated. Alternative methods when using it are the Shepherd's Length Composition Analysis (Shepherd 1987a) Projection Matrix (Basson et al. 1988), or Length/Weight Frequency Analysis (ELEFAN) (Pauly 1987). The Hoenig (Hoenig and Hanumara 1982) and Pauly (Pauly 1987) functions are variations of the von Bertalanffy model and take into account seasonal growth. A score function (goodness of fit) is used in LFDA to derive a number that shows how likely it is that the data come from a stock with that growth function. The higher the function (approaching 1) the more likely it is the data come from a stock with that growth function.

The Pauly model was used in the present study because it is geared towards populations that stop growing completely at certain times of the year. This was determined for the present study from observations of changes in size classes and mean population weight over the year. For seasonal growth, C and t_s (the start of convex segment of oscillation) were estimated from the data as well as K, the rate at which weight approaches infinity (W_∞) and actual W_∞. In the present study, the model was run several times, altering K and W_∞ to cross-check score maximisation (Table 1). This process was performed for the non-seasonal ELEFAN to give a baseline comparison of model parameter maximisation for the Hoenig and Pauly seasonal model. The Pauly seasonal model was then used in subsequent steps and model maximisation of parameters compared with non-seasonal parameter estimates.

The catch curve total mortality rate was also estimated for each distribution by fitting a regression line through the von Bertalanffy catch curve. Z was estimated for each sample and the mean and standard error given.

Table 1. Model output of growth parameters for *Australostichopus mollis* and model maximisation for goodness of fit. Where, K = growth rate, W_∞ = asymptotic weight, t_0 = time at which weight = 0, t′ = real age (t) less total no growth time to age t, NGT = duration of non growth within a year, T_s = start of convex segment of oscillation with respect to t = 0.

	Step 1 **K vs W_∞**	**Step 2** **C vs t_s**	**Step 3** **NGT vs t_s**	**Step 4** **K vs W_∞**
K	1.12	1.38	1.0	1.22
W_∞	133	125	140	133
C	0.46	0.44	NA	NA
t_0	-0.96	0.91	-0.39	-0.31
T_s	0.27	0.06	0.17	0.19
NGT	NA	NA	0.29	0.30
Maximised at:				
Fit	0.89	0.89	0.95	0.96
K	1.33	NA	NA	1.37
W_∞	125.90	NA	NA	129
C	NA	0.46	NA	NA
t_0	-0.93	-0.92	-0.40	-0.94
t_s	NA	0.27	0.19	NA
NGT	NA	NA	0.30	NA

Growth function

Calculated growth parameters were used to estimate weight at time t (W_t) and construct the growth curve. The general growth equation is:

$$W_t = W_\infty \times (1-e^{-q})$$

In the Pauly seasonal growth equation q is:

$$q = K(t'-t_0) + K/Q[\mathrm{Sin}Q(t'-t_0) - \mathrm{Sin}Q(t_o-t_s)]$$

Where $Q = 2\pi(1-NGT)$
K = growth rate
W_∞ = asymptotic weight
t_0 = time zero (born)
t′ = real age (t) less total no growth time to age t
NGT = duration of non-growth within a year
t_s = start of convex segment of oscillation with respect to t = 0

Results

The majority of *A. mollis* within the population were in the 100–119-g size class (Fig. 1). The next prevalent size class was 120–139 g. Mean population weight declined to April, reaching 107 ± 3.3 (CI) g and then increased to 127 ± 4 (CI) g in October, the final sampling date (Fig. 2). Over the year, 1,654 individuals were sampled, consisting of 297 in sample 1 October, and 221, 218, 172, 203, 292, and 251 for

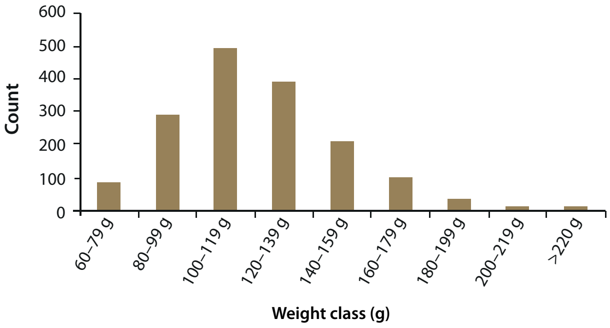

Figure 1. Total numbers of *Australostichopus mollis* from each 20-g size class recorded over all seven days of surveying (n = 1654).

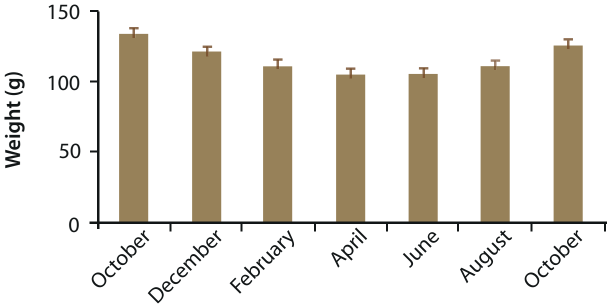

Figure 2. Mean weight (g) of *Australstichopus mollis* for each sampling date (±SE).

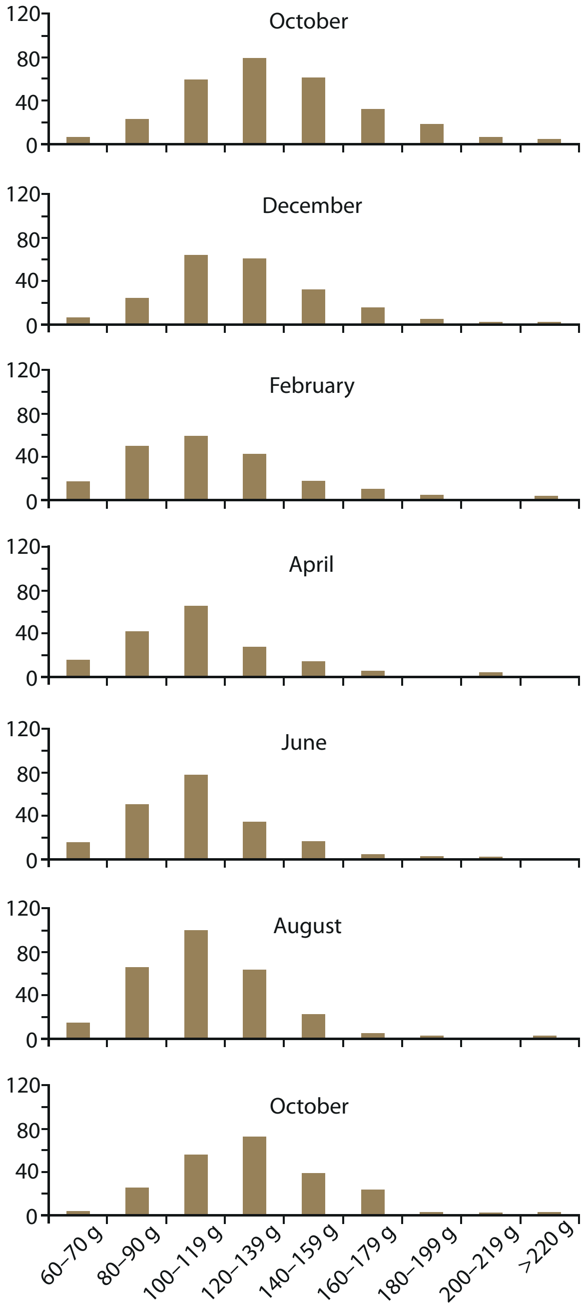

Figure 3. Changes in numbers of *Australstichopus mollis* for each size-frequency distribution over the year of sampling.

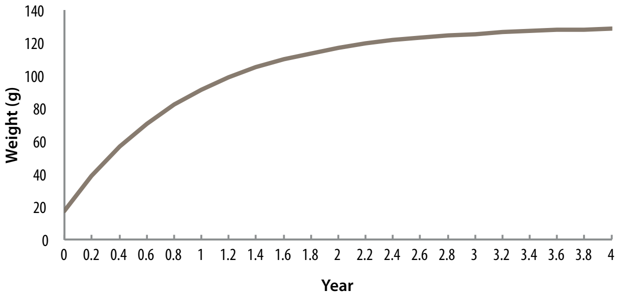

Figure 4. von Bertalanffy population model estimates of size-at-age for *Australostichopus mollis* from parameters calculated for the Pauly seasonal growth function.

December, February, April, June, August and October, respectively.

In general, an overall increase in population numbers was observed, moving through adult cohorts for the 80–99, 100–119, and 120–139-g size classes (Fig. 3). Numbers over the 120–139-g size class were less for April, June and August. Numbers in the 100-119 g size class were consistently high. Numbers in the size classes between 120–139 g and 160–179 g decreased from December through to April of the following year, followed by an overall increase on subsequent sampling dates.

Estimated parameters were inserted into the von Bertalanffy growth equation with the Pauly seasonal modification and weight-at-age calculated for proportions of the year across years (Fig. 4). Weight at year zero was 17 g but t_0 was calculated at - 0.97 for model maximisation. This assumed that at some prior time they were eggs, larvae and subsequently settled, adopting the early juvenile stage prior to being a juvenile. This period of time is not known but can be approximated from knowledge of the larval cycle and early juvenile period, and may take anywhere between four months to one year (Morgan 2009b; Slater and Jeffs 2010; Stenton-Dozy and

Heath 2009). Growth of *A. mollis* after one year was estimated at 100 g, reaching 120 g after two years. Subsequently, asymptotic weight tended towards 130 g at three years.

The age composition of weight frequencies was calculated by using the fitted growth curve to delineate boundaries between weights-at-age and then slicing the weight-frequencies at those boundaries (Fig. 5). t_0 was constrained to lie between -1.0 and 0.0, meaning that nominal ages were not the same as true ages. Both the Hoenig and von Bertalanffy models estimated similar weights at years 0 and 1. Weights for year 0 ranged between 20 g and 50 g. This was indicative of the proportion of the population in its first year of growth. Weights for year 1 ranged between 70 g and 140 g. This was indicative of the proportion of the population in its second year of growth.

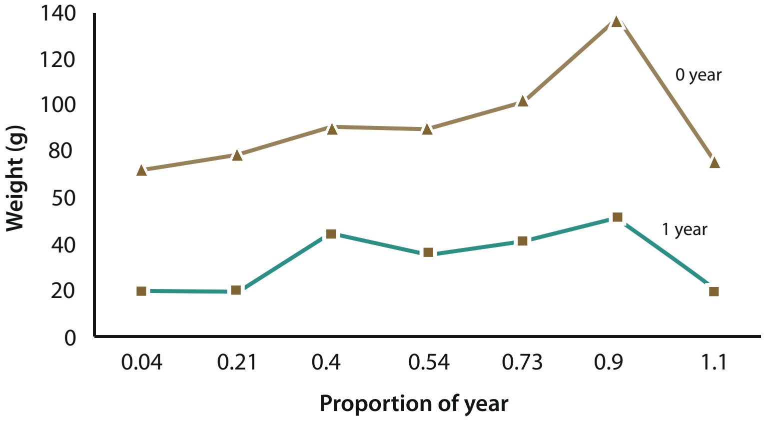

Figure 5. Population age composition of weight frequencies for *Australostichopus mollis* calculated from the fitted growth curve to delineate boundaries between weights at age and then slicing the weight frequencies at those boundaries. t0 was constrained to lie between -1.0 and 0.0, meaning that nominal ages might not be the same as true ages.

The total mortality rate Z was based on non-seasonal growth. This is not usually a problem because most stocks growth, although not maximised, can be reasonably described by the non-seasonal von Bertalanffy model. The Beverton Holt instantaneous mortality rate (Beverton and Holt 1956) describes the relationship between weight, weight at first full exploitation, the von Bertalanffy parameters and the total mortality rate Z. Lc is the first weight class fully exploited and can be interpreted from the data. For *A. mollis*, instantaneous mortality (natural mortality M) was 0.58 (Fig. 6). Maximum total population mortality rate was $-1.5\ \mathrm{yr}^{-1}$ in October. Because it was likely there were only two age classes in the data, mortality rates should be interpreted with caution and may be influenced by seasonal growth limitation.

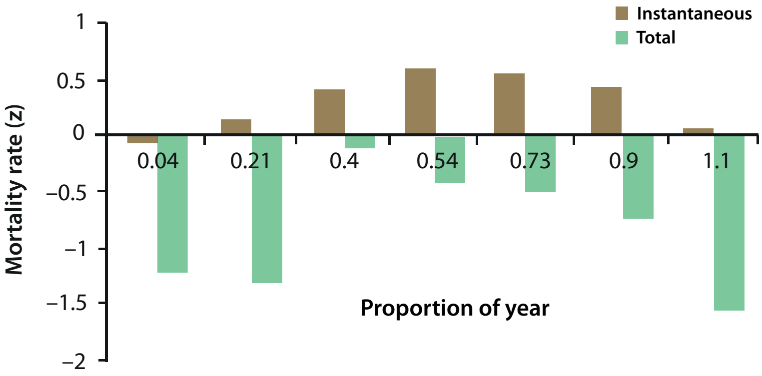

Figure 6. Instantaneous (natural) and total population mortality rates of *Australostichopus mollis* at each sampling date (Bev Holt K = 1.22; W_∞ = 133; Lc = 60; mean = 0.30; std err = 0.10; catch curve K = 1.22; W_∞ = 133; mean = -0.84; std err = 0.08).

Discussion

Size is a tradeoff between growth and survival, which is impacted on by the environment a species has adapted to over time. This has been explained previously for sea urchins relative to the amount of stress and disturbance they are exposed to in the environment they have adapted to (Lawrence and Bazhin 1998). For instance, ruderal species in environments where they are exposed to low stress and high disturbance (Carlow 1984; Lawrence and Bazhin 1998; Lawrence and Herrera 2000) will exhibit faster growth rates but decreased survival, and will put more resources towards reproduction but maintain low assimilation efficiency (Table 2). Similarly, for sea cucumbers in temperate coastal regions where food may be seasonally abundant (Hammond 1982; Sonnenholzer 2003) and the area exposed to high disturbance, mortality may be high. In this environment the proportion of weight reached at first reproduction relative to weight at one year may also be high (i.e. sexual maturity is reached before or near one year). This is typical of a species such as *A. mollis* where in the present study size in the second year of growth was modeled at 100 g. For this species in this location, size at sexual maturity was greater than 75 g (Sewell 1987). This relationship between size and sexual maturity may differ in more stress-tolerant sea cucumbers in an environment with low disturbance (i.e. some deep-water species in sheltered environments that are food limited). Survival may be high but growth rates are slow and time to reproductive maturity as a proportion of size at one year is extended.

Once reproductive maturity is reached, sea cucumber weight can fluctuate seasonally relative to the allocation of resources to reproduction and/or growth and metabolism (Rutherford 1973), as was found for *I. fuscus* (Herrero-Perezrul and Reyes-Bonilla 2008). This relationship between population weight and reproductive maturity has been determined for sea cucumbers such as *Holothuria scabra*, *H. nobilis*, *Actinopyga echinites* and *Thelenota ananas* (Table 3). In the present study for *A. mollis*, mean population weight also varied seasonally between 107 g and 135 g, depending on the time of the year. Furthermore, in another study a marked growth limitation for *A. mollis* juveniles was found to occur between six and nine months after caging either due to an increase in biomass or seasonal growth limitation (Slater and Jeffs 2010). In both studies, this seasonal weight loss in *A. mollis* occurred during the winter months of May, June and July. In another study, the mean population weight of *I. fuscus* was 386 g with a maximum adult weight of 815 g but this varied significantly between months, depending on reproductive condition (Herrero-Perezrul and Reyes-Bonilla 2008). Toral-Granda

Table 2. Life history characteristics of *Australostichopus mollis* affected by the environment a species has adapted to and whether they increase or decrease (summarised from: Carlow 1984; Lawrence and Bazhin 1998; Lawrence and Herrera 2000).

	Ruderal Low stress High disturbance	**Competitive Low stress Low disturbance**	**Stress-tolerant High stress Low disturbance**
Growth	+		–
Survival	–		+
Reproductive effort	+		–
Assimilation efficiency	–		+
Proportion of maximum weight at first reproduction	<		>
Proportion of reproductive weight at one year	>		<

Table 3. Sea cucumber species and the ratio of drained weight at first reproduction (DW 1st Repro) to population drained weight (Pop DW) converted to a percentage (%).

Species	**DW 1st Repro**	**Pop DW**	**%**	**Authors**
Holothuria scabra	130	350	37	Conand 1989
H. scabra versicolor	320	970	33	Conand 1989, 1993
H. fuscogilva	900	1460	62	Ramofafia et al. 2000
H. nobilis	580	1240	47	Conand 1989, 1993
Actinopyga echinites	130	300	43	Conand 1989
Thelenota ananas	1150	1980	58	Conand 1989. 1993
Parastichopus californicus	50	313	16	Cameron and Fankboner 1985, 1989
Australostichopus mollis	91	140	65	Raj 1998 (South Island)
A. mollis	75	130 (W)	58	Sewell 1990, 1992, present study (North Island)
Stichopus japonicus	50	120	41	Ito 1995; Ito and Kitamura 1998
S. chloronotus	52	110	47	Conand 1988; Uthicke 1997; Conand et al. 1998
Isostichopus fuscus	367	500	73	Herrero-Perezrul et al. 1999

W = wet weight of whole animal (green weight) and Martinez (2007) also found that *I. fuscus* was sexually active throughout the year and that where condition indices relative to size were highest, this reflected a peak in reproductive condition. However, apart from work by Conand (1988) and more recent studies (Herrero-Perezrul and Reyes-Bonilla 2008; Toral-Granda and Martinez 2007) little is known about how size-at-age or the rate at which a particular size is approached interacts with any variation in reproductive condition or weight fluctuations across seasons for sea cucumbers.

Size at age can vary between and within years. In the present study, *A. mollis* consisted of two age classes, year 0 and year 1, with a size at the start of year 0 of 17 g. It is also assumed that at some time prior, as estimated by the parameter t_0, individuals in the population of *A. mollis* were eggs, larvae and early juveniles. Previously, for both *T. ananas* and *S. chloronotus*, t_0 was -0.672 and -0.251, respectively (Conand, 1988) so estimates of t_0 for *A. mollis* in the present study are not uncommon. Estimates of t_0 from -0.4 to -0.97 put this period anywhere from about four months to one year. *A. mollis* growth after six months in cages ranged from 32 g to 100 g after starting at an initial size of 23 g (Slater and Jeffs 2010).

A. mollis hatchery bred juveniles have been found to reach 50 mm in six months from initial spawning, weighing approximately 4 g (Stenton-Dozey and Heath 2009). In another study, the sea cucumber *Cucumaria pseudocurata* was found to have a large increase in growth rate during the first year subsequent to recruitment (Rutherford 1973), which is also not uncommon in ruderal unstable environments. Similar to *A. mollis*, a decrease in growth rate was observed after this initial year. In the present study, very few individuals were found weighing less 60 g, so it was assumed they recruited into the population near or around this size (Sewell 1990). In addition, for *A. mollis* in year 1, a large proportion of total growth occurred as was found for *A. mollis* juveniles in caging experiments (Slater and Jeffs 2010). Evidence suggests that variation in size-at-age may be a consequence of the timing of spawning and variable growth rates of individuals within the population prior to recruitment. This may account for the variability in size range within year 0 and year 1 for age slicing and the estimate of t_0 in the von Bertalanffy model.

In addition, within a species, geographic distribution size-at-age is not always consistent. For example, in *I. fuscus* size at sexual maturity was 367 g and this was reached after five years, with asymptotic population weight being 575 g (Herreo-Perezrul et al. 1999; Reyes-Bonilla and Herrero-Perezrul 2003). Conversely, Toral-Granda and Martinez (2007) found size-at-maturity in a different location to be 165 g drained weight but age was not known. For *A. mollis* on the South Island of New Zealand, size at sexual maturity was greater than 90 g drained weight, or approximately 100 g wet weight, with a mean population weight of 140–150 g drained weight (Raj 1998). However, size-at-age and the rate this was approached was not known. On the North Island of New Zealand, size at sexual maturity of *A. mollis* was greater than 75 g (Sewell 1987) and occurred at less than one year. This size range is smaller than those from the South Island. Despite this, for both North and South Island populations, size at reproductive maturity of *A. mollis* accounted for approximately 60% of mean population weight (Table 3). However, for a species over a broad geographic scale, without knowledge of both growth rate and size at age within a habitat it is difficult to determine life span.

The rate (K) at which asymptotic population weight was reached in *A. mollis* was estimated to be as high as 1.37 yr^{-1} in the maximised model but was as low as 1.0 yr^{-1} in model iterations. In a previous study for *H. floridana* the rate of K was 0.21 yr^{-1} (Fuente-Betancourt et al. 2001) while for *T. ananas* and *S. chloronotus* it was 0.199 yr^{-1} and 0.449 yr^{-1}, respectively (Conand 1988). Although *A. mollis* is temperate and *S. chloronotus* is sub-tropical, they appear to have similar size characteristics although *A. mollis* has a higher value for K. Typically, short-lived species such as *A. mollis* that exist in distinctly ruderal environments have a high value of K (> 1.0 yr^{-1}) and approach asymptotic population weight quickly (Sparre et al. 1989). For *A. mollis*, asymptotic population weight occurred at three years while for *S. chloronotus* this took six years. Consequently, it is expected that K for *A. mollis* would be approximately double that of *S. chloronotus*. However, much larger species such as *T. ananas* are long lived and usually have relatively low values for K. In such cases it could be expected that life span is extended considerably. For *T. ananas*, age at asymptotic population weight was 14 years while K was as low as 0.199 yr^{-1} (Conand 1988). However, in ruderal environments such as the present study, an increase in the rate at which asymptotic population weight is approached has significant consequences for survival. In these environments as life span is extended individuals are increasingly exposed to the risk of mortality.

A high rate of mortality is due to the tradeoff between achieving fast growth and reduced survival in unstable ruderal environments (Carlow 1984; Lawrence and Bazhin 1998; Lawrence and Herrera 2000). Both *H. atra* and *I. fuscus* live in such environments. For *H. atra*, over a year a loss of 50–70 % of the total population occurred (Ebert 1978). For *I. fuscus* animal condition (Kn) in relation to post-reproductive maturity declined, reflecting a corresponding decline in the health of animals (Herrero-Perezrul and Reyes-Bonilla 2008). Typically, for *I. fuscus*, the total mortality rate (Z) was 0.70 yr^{1} (Reyes-Bonilla and Herrero-Perezrul 2003). For *I. fuscus*, the instantaneous natural mortality rate (M) was 0.67 but the median was 0.354 (Reyes-Bonilla and Herrero-Perezrul 2003). The natural mortality rate of *I. fuscus* was also found to be 0.174 (Hearn et al. 2005), and for *H. floridana* was 0.72 (Fuente-Betancourt et al. 2001). In the present study, the instantaneous mortality rate, the natural mortality rate of *A. mollis*, was 0.58 but was also close to 0.0 at certain times. Note that for sea cucumbers, due to several anti-predator characteristics, predation on adults is thought to be rare (Francour 1997). Although in the present study both total population mortality rate and the instantaneous mortality rate appeared high, these numbers are likely confounded by the seasonal variation in weight that occurs within the population and the lack of distinct juvenile cohorts recruiting into it. Despite this, evidence suggests that for sea cucumbers that live in increasingly ruderal, unstable, and dynamic environments, the growth rate will increase, but mean adult size will be reduced while mortality rates will be high but seasonally variable as appears to be the case for *A. mollis*.

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