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Age, Growth and Population Dynamics

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1. Introduction

Many sea turtle stocks are in decline worldwide due to excessive harvesting and destruction of nesting and foraging habitats (National Research Council 1990, Bjørndal et al. 1993, Limpus 1993, Horikoshi et al. 1994). Yet population abundance for many stocks can display stochastic fluctuations with no apparent long term trend (National Research Council 1990, Limpus and Nicholls 1994).

How are we to know then whether a stock is really at risk and what risk management strategies might be appropriate for protection of the stock. These are challenging questions that cannot be resolved without a thorough understanding of sea turtle growth and population dynamics. Age and size are related components of somatic growth, which itself is a major determinant of population dynamics and macroevolutionary change.

Therefore, we review in broad terms a wide range of studies on age, somatic growth and the population dynamics of sea turtle stocks. Firstly, we present an overview of some of the major methodological issues relevant to understanding sea turtle growth and population modelling. This section is essential to appreciate the methodological themes apparent in the remaining sections. Many of the methods used need careful scrutiny of the underlying statistical properties and assumptions. Therefore the main emphasis in this review is on methodological issues.

Then we review critically a compilation of sea turtle growth studies arranged in a classification table providing a framework for grouping similar approaches. Next we discuss the complementary approaches of comparative life history analysis and comparative demography as a precursor to population dynamics. In the last section we review critically all known studies on sea turtle population dynamics also arranged in a classification table. We conclude with a brief overview of the review focusing on recurrent methodological issues.

2. Methodological background

2.1 Sampling issues

Ecological studies are based on many presuppositions including two key sampling design issues – (1) the stock is distinguishable over time and space and (2) the demographic processes of that stock are time invariant. The first design issue is reasonably well understood but the second issue of implicit time invariant sampling is very poorly understood in most ecological research let alone in sea turtle studies.

2.1.1 Demographic unit

The identification of discrete demographic units is fundamental to understanding growth dynamics, population dynamics and macroevolutionary change. Recent studies on growth and dispersal in the epipelagic developmental habitat (Zug et al. 1995, Bowen et al. 1995) as well as in foraging areas (Limpus et al. 1994a,b; see Miller 1994) are helping to provide a more complete description of sea turtle ontogeny and spatial dispersion patterns. So there is no apparent reason why ecological modelling of sea turtle stocks would take a restricted perspective of sea turtle demography.

However, identifying a discrete demographic unit poses a major challenge. Sea turtle breeding stocks are likely to comprise multiple rookeries within a region while foraging areas and developmental habitats comprise a mix of turtles from several genetically distinct stocks (Broderick et al. 1994, Bowen et al. 1995). But the intermingling of individuals from different stocks in different habitats makes it difficult to distinguish individuals from each stock and so makes it difficult to recognise the spatial dispersion

pattern for each stock. It is important therefore to be able to recognize individuals from the different stocks in these separate habitats. The main reason being to link individuals with their correct breeding, developmental and foraging habitats so that the focus of a study and conclusions are relevant to that stock.

It is now possible to distinguish discrete sea turtle demographic units across breeding, foraging and developmental habitats using a mark-recapture program combining stock-specific genetic markers and physical individual tagging (Broderick et al. 1994, Bowen et al. 1995).

Assuming demographic independence for distinct stocks and the capacity to recognize each stock it follows that the appropriate management and population modelling focus should be a genetically distinct breeding stock and its associated developmental habitats and foraging areas. For practical purposes the management focus might in some cases be limited geographically because of trans-boundary jurisdictions. Nevertheless, all sea turtle growth and population studies should be referenced to a genetically distinct stock enabling a better understanding of the full spatial dispersion pattern of each stock.

2.1.2 Demographic sampling design

Estimates of demographic rates such as mortality, growth and recruitment rates are a key part of modelling population dynamics. However, demographic processes are complex time-dependent functions comprising three confounded time effects (age, year, cohort). In other words there is natural variability in demographic rates attributable to age-specific, inter-annual and cohort specific factors. Year effect is considered an environmental factor while the cohort effect is usually considered to be a genetic factor.

Confounded time effects can result in biased estimates so demographic analyses need to uncouple the time effects by accounting for age, year and cohort factors in say a tabular model known as a lexis diagram (Keyfitz 1985) or a statistical model (Brillinger 1986). Accounting for time-dependent effects has rarely been done in sea turtle studies. It is not always possible to uncouple the time effects in many studies. For instance, Tucker et al. (1995b) in one of the rare ecological studies to recognize the issue of confounded time effects proposed a method to account for inter-annual growth rate variation in slider turtles. They concluded correctly that failure to account for this time effect would lead to incorrect growth rate estimation. Age was determined by independent means but the authors seem unaware that both age and year were confounded due to the implicit cross-sectional sampling design used. It is important to understand that there are three time effects involved and if it is not possible to uncouple all of them that you must be well aware which factors are confounded.

Any form of time-dependent demographic sampling that involves cross-sectional sampling (random sampling with replacement) of a turtle stock will confound the main effects of age and cohort as well as the interactions. Longitudinal sampling (repeated sampling on the same individuals) will confound age and year main effects and interactions. Mixed longitudinal sampling (sampling with partial replacement) will confound only the interactions if age is known or will confound year, cohort and interactions if age is unknown. All sea turtle growth studies are based on one of these sampling schemes with major implications for interpretation. A useful discussion of age, year and cohort effects in relation to implicit sampling design is presented by Berger (1986) while Fitzhugh (1975) gives a useful classification of data types used in growth studies.

2.2 Mark-recapture procedures

Metal tagging of flippers is the most common approach used for mark-recapture programs designed for long term monitoring of individual turtles (Hendrickson 1958, Balazs 1982, Le Gall et al. 1986, Bjørndal et al. 1993, Limpus 1992, Limpus et al.

1994a,b). Over time a detailed mark-recapture profile is compiled for each turtle comprising morphometric measurements at first and subsequent recaptures, time of first capture, time-at-large since first capture and in some cases determination of sex, maturity and reproductive status derived from visual examination of gonads using laparoscopy (Wood et al. 1983, Limpus and Read 1985).

These profiles provide the basis for estimating demographic parameters needed for population modelling such as mortality rates (Bjorndal 1980, Le Gall et al. 1986, Limpus 1992b, Heppell et al. 1996), recruitment rates (Parmenter and Limpus 1995), inter-habitat dispersal rates (Limpus et al. 1992), annual remigration rates (Limpus et al. 1994c) and sex-, size- and age-specific growth rates (Chaloupka and Limpus 1995a). The collection of demographic information on individual turtles requires a reliable means of capture and marking to enable recognition at recapture. Clearly the reliability of the marking methods is a concern for long term mark-recapture programs.

2.2.1 Marking methods

The methods of capture of individual turtles range from passive capture of cold stunned turtles or nesting females to active approaches used in shallow water such as netting, beach jumping and the turtle rodeo technique (Limpus and Read 1985). Deeper water capture is usually done using SCUBA. Miller (1994) provides a thorough descriptive overview of the range of methods used to catch sea turtles in foraging grounds and the specific data oriented purpose of each method. There have been no studies of the demographic sampling bias associated with any of these capture methods – all studies presume that the sample obtained is an unbiased representative sample of the population under study.

Following capture a variety of tagging devices have been used to mark individual sea turtles depending on cost, study purpose and ontogenetic stage. Hatchlings or juveniles have been marked with mutilation notches (Limpus et al. 1994a,b), injected with magnetically coded wire tags (Schwartz 1981), autografts (Wood and Wood 1993) or plastic tags (Bjorndal et al. 1994). Immature and adult turtles are usually marked with one or more flipper tags of various material such as plastic (Green 1993, Wood and Wood 1993), monel (Hendrickson 1958, Le Gall et al. 1986, Bjorndal and Bolten 1988a, Boulon 1992, Collazo et al. 1992, Bjorndal et al. 1993, Green 1993, Klinger and Musick 1995), inconel (Balazs 1982, Limpus 1994a, Caillouet et al. 1995) or titanium (Limpus 1992, Wood and Wood 1993).

Other forms of post-natal marking include PTT tags (passive integrated transponders) where metal tags were unable to be secured (Parmenter 1993) and radio or satellite biotelemetry for tracking in real time local movement (Tucker et al. 1995a, Plotkin et al. 1995) or long distance dispersal (Papi et al. 1995). Skeletal elements have also been marked by injection of OTC to record a bone growth layer benchmark suitable for skeletochronological aging (Klinger and Musick 1992 – see section 2.3).

2.2.2 Tagging protocols

Most sea turtle monitoring programs use multiple tagging with subsequent replacement protocols although a few have relied on single tagging such as for green turtles nesting in Malaya and Sarawak (Hendrickson 1958), green turtles nesting at Tromelin and Europa in the Indian Ocean (Le Gall et al. 1986) and for recaptured head started Kemp's ridleys released in the Gulf of Mexico (Caillouet et al. 1995).

While many long term sea turtle monitoring programs have used multiple tagging protocols most of them have also used monel alloy tags, which are known to corrode rapidly in sea water (Henwood 1986, Limpus 1992a). Clearly, studies that used single monel tagging (Hendrickson 1958, Kowarsky and Capelle 1979, Limpus and Walter 1980, Bjorndal and Bolten 1988b, Le Gall et al. 1984, Le Gall et al. 1986, Caillouet et

al. 1995) are most at risk although Caillouet et al. (1995) have also used single inconel tags and Limpus has long since moved to multiple titanium or inconel tagging (Limpus 1992, Frazer et al. 1994, Limpus et al. 1994a,b). Single tagging even if it is an inconel tag (Caillouet et al. 1995) or a titanium tag (Wood and Wood 1993) is not a prudent practice. Plastic tags are known to deteriorate rapidly in sea water probably resulting in low tag retention rates (Limpus 1992a).

Both inconel and titanium tags have outstanding long term durability in sea water (Balazs 1982, Limpus 1992a). However, both monel and inconel are alloys containing nickel, which is a known antifouling agent. Titanium on the other hand has no antifouling properties although it also has no known toxic properties. Limpus (1992a) has noted that titanium tags on recaptured sea turtles in the Great Barrier Reef are often covered with barnacles, which he attributes to potential tag loss. Wood and Wood (1993) suggested an association between titanium tags and fibropapillomas on recaptured head started green turtles released from the Cayman Islands. Studies using both inconel and titanium tags such as Limpus (1992b) and Limpus et al. (1994a,b) conducted in accordance with a properly designed experimental protocol could help to resolve these issues.

Clearly, more research on tag design, material technology and tag retention rates is needed but it might well be that inconel and perhaps titanium are the preferred materials for long term monitoring of sea turtle stocks.

2.2.3 Tag loss analysis

Sea turtle tag loss is a complex function of time dependent competing risks (Henwood 1986, Limpus 1992a) such as – (1) incorrect application of tag, (2) loss due to mechanical stress at nesting or from courtship biting, (3) tissue necrosis, (4) tag corrosion, (5) censored record due to death and unrecovered tag. These risk factors suggest why multiple tagging with replacement is a sensible tagging protocol.

The first two factors reflect an early failure period, tissue necrosis reflects variable but probably relatively early failure while corrosion and censoring reflect a later failure period. The underlying hazard function is then nonmonotonic or multimodal where tag loss is high initially due to early risk factors followed by a period of decreasing risk and then followed later by a period of increasing risk due to corrosion and observation censoring as the both the tag and the turtle age.

This hazard function explains the finding in Henwood (1986) that his analysis predicted far higher loss rates than would seem consistent with recorded reneesting rates of tagged females. The linear regression model used by Henwood (1986) assumes a constant hazard function, no competing risks and no censoring processes and is not suitable for analysis of tag retention.

Limpus (1992a) in a detailed analysis of tag retention risk used a logit regression approach, which assumes a monotone increasing hazard. He assumed no censoring processes and the implicit hazard function would be inappropriate if an early failure period occurs. Censored regression models with risk-specific nonmonotone hazard functions (Lawless 1982) might be worth considering in future analyses. Nonetheless, Limpus (1992a) provided a major contribution to tag loss analysis supporting confidence in results obtained from his long term tagging studies of Great Barrier Reef loggerhead and green turtles stocks.

2.3 Skeletochronology

Periodic marks or growth checks on hard parts such as scales or bones have been used to estimate vertebrate age for almost 100 years (Carlander, 1987). The procedure assumes amongst other things that (1) a constant proportional relationship exists

between hard part growth and somatic growth and (2) that discernible periodic growth rings or annuli are deposited at regular constant time intervals. Zug et al. (1986) reviewed the history of the use or attempted use of bony rings to estimate age (skeletochronology) in sea turtles. The future of skeletochronology for estimating sea turtle ages rests with resolving three issues – (1) validation of universal annual deposition of growth layers, (2) development of a robust method to correct age estimates for growth layer loss and (3) validation of constant proportional allometry between bone growth and somatic growth to enable application of length-at-age back calculation methods.

2.3.1 Growth mark validation

Zug et al. (1986) used the humeral bones to estimate age and growth for northwestern Atlantic loggerheads. They assumed that growth zones apparent following histological processing of the bone were deposited on an annual basis although Frazier (1982) had mixed success previously in validating the annual nature of bony rings in sea turtles.

Klinger and Musick (1992) have validated the annual nature of the humeral growth layers in loggerheads using oxytetracycline injection. Several turtles were subsequently stranded dead or were recaptured live by fishermen after being at large for up to four years. Humeri were removed from dead animals and processed according to Zug et al. (1986). The number of growth rings deposited beyond the fluorescent OTC benchmark were then counted. Live recaptured turtles were anaesthetized and humeral bone biopsy samples were taken and histologically processed as in whole humeral sections (Klinger et al. in press). The results of this study showed definitively that one growth layer was deposited for each year a turtle was at large for this stock after OTC marking.

Annular growth zones in the humeri of a wide size range of western North Atlantic loggerheads have now been validated. In addition, growth zones have been validated in a small sample of *Lepidochelys kempi* (Klinger and Musick, unpublished). It remains to be seen whether such zones are formed on an annual basis over the entire size range of *Lepidochelys kempi*, or for small pelagic loggerheads.

Frazier (1985) also used the OTC method to attempt to validate the nature of growth zones in a captive group of green turtles, but had poor results. Zug et al. (1986) suggested that this was likely because the growth rates were accelerated in captivity and so that the normal pattern of bone growth might have been disrupted. This is an important point because supposedly aseasonal environments such as the tropics may not induce strong seasonal pulses in growth commonly found for more warm temperate species such as loggerheads or Kemp's ridley – the two species subject to most aging studies. Annular layers have yet to be validated for sea turtle species with a tropical distribution pattern such as greens and hawksbills.

2.3.2 Layer loss correction protocols

Growth layer resorption in skeletal elements has been found to occur in post-pelagic growth phases of loggerheads, Kemp's ridleys and leatherbacks (Zug et al. 1986, Klinger and Musick 1992, Zug et al. 1996, Zug and Parham 1996, Parham and Zug 1997). Zug et al. (1995) have also shown that growth layer resorption also occurs in pelagic loggerheads less than 20cm CCL or about 2 years old caught in the North Pacific high seas drift-net fishery. Therefore, it seems likely that growth layer resorption occurs in all post-natal growth phases of sea turtles.

Zug et al. (1986) proposed originally a simple absolute growth rate averaging method to compensate for growth layer loss when determining age estimates for post-pelagic loggerheads. However, this method may overestimate the number of layers because growth may be faster and growth layers may be wider in younger, fast-growing turtles than in older, slower-growing turtles (Zug 1990).

Other adjustment methods to correct for growth layer loss have since been developed and are now more widely applied – (1) correction factor protocol (Klinger and Musick 1992, 1995; Zug et al. 1996, Zug and Parham 1996, Parham and Zug 1997), (2) regression growth protocol (Zug et al. 1995, Parham and Zug 1997) and (3) the ranking protocol (Zug 1990, Zug et al. 1995, Zug et al. 1996, Parham and Zug 1997). The correction factor and regression growth protocols are based on several assumptions related to constant relative growth rates predicated on a von Bertalanffy growth function and in some cases application of the Fraser-Lee back calculation function (see Klinger and Musick 1992, Parham and Zug 1997). The use of the Fraser-Lee BCF is also discussed in the next section concerning length-at-age estimation. The Zug (1990) ranking protocol is far simpler and based on fewer implicit assumptions. Nonetheless, all three methods require further validation and development to warrant confidence in the age estimates derived using these adjustment methods.

2.3.3 Length-at-age back calculation

The standard Fraser-Lee back calculation method was used by Klinger and Musick (1992, 1995), Zug et al. (1996) and Parham and Zug (1997) to derive loggerhead and Kemp's ridley length-at-age records. The specific reason for back calculation other than for growth layer loss adjustment was not clear but is presumed to be for increasing the sample size for fitting an age-size growth function. The sample could also include age-length estimates for lengths not observed in the study.

Length back calculation derives multiple age-length measurements for each individual depending on the ontogenetic stage reached by the individual at time of biopsy or death. Back calculation in theory then represents mixed longitudinal sampling, which is desirable. However, it has been common practice to use the standard Fraser-Lee BCF providing only a length estimate at the earliest discernible growth mark (Klinger and Musick 1992, 1995; Zug et al. 1996; Parham and Zug 1997). This practice yields only mixed cross-sectional data at the expense of discarding valuable growth information.

Zug et al. (1996) in an analysis of Kemp's ridley growth also used Fraser-Lee derived back calculated lengths for fitting the Fabens size-based analogue of the von Bertalanffy growth function. The Fabens analogue is not appropriate for determining an age-length function (see 2.4.3; Francis 1988). Moreover, the parameter form of the von Bertalanffy growth function fitted to all these age-length data sets is known to have poor statistical properties (Ratkowsky 1986, 1990). These issues are discussed in more detail in section 2.4.

There appears to be much confusion in the sea turtle skeletochronological literature regarding the correct approach for using proportional back calculation functions (BCFs). The main problems seem to be due to a misunderstanding of the following – (1) implicit proportionality hypothesis, (2) correct form of the standard Fraser-Lee equation, (3) potential of the general Fraser-Lee equation to derive multiple length-at-age measurements per individual, (4) correct linear regression to use depending on the particular back calculation function used.

Assuming a scale proportional hypothesis, a regression of the data set comprising the humerus radial length (y variable) and straight carapace length (x variable) recorded from each individual at capture should be applied (Francis 1990). Ricker (1992) argues that the order of (y) and (x) is irrelevant so long as a symmetrical linear regression model such as the reduced major axis model is used to derive the parameter estimates.

If the fitted functional relationship is linear then it is possible using the regression parameter estimates to derive back calculated length estimates for a specific individual at all previous ages indicated by the growth checks using an appropriate BCF such as the general Fraser-Lee equation (see Francis 1990). This generates a set of length-at-age

data with variable number of length-age records per individual for fitting an age-size growth function. There is of course no necessity to use a regression model in the first place since biologically determined values where available could just as validly be used in any proportional BCF (see Ricker 1992 and references therein).

Irrespective of method, current back calculation functions do not take into account the time-dependent nature of the relationship between skeletal and somatic growth rates. Future sea turtle aging models using skeletochronology and back calculation will need to evaluate the assumptions of proportionality and time invariant growth rates.

2.4 Growth

2.4.1 Growth measurement

Somatic growth for a mark-recaptured turtle is described in terms of length or weight with length measured as either straight carapace length (SCL) or curved carapace length (CCL). There seems little basis for preferring SCL over CCL measurements except perhaps for leatherbacks where CCL is more appropriate (see Parham and Zug 1996).

Somatic growth is a dynamic process and can be approximated in terms of either absolute growth rates or specific growth rates (see Ricker 1975). Absolute growth rates are described as change in size measured as length or weight recorded over a time interval of variable duration. Specific growth rates are described as the absolute growth rate per unit size estimated simply as the logarithmic absolute growth rate.

Strictly speaking these are only really rates if the time interval is a constant unit interval. In sea turtle studies annual growth is usually measured as the average rate of size gain recorded over the time interval between first capture and recapture, which is rarely if ever one year. This presumes that the absolute growth rate is locally linear or constant across the time interval. For small time intervals this might not be a serious issue. But as the interval between recaptures increases then it might well be important since growth is unlikely to be linear causing significant growth rate measurement error. Chaloupka and Limpus (1995a) found that the recapture interval measured in years was not a significant factor affecting absolute growth rates in their study of the southern Great Barrier Reef green turtle stock. This was a limited test of this problem and needs to be tested for each specific study before mark-recapture interval could be discounted.

Most studies of sea turtle growth have used absolute growth rates but Bjørndal and Bolten (1998a) used both absolute and specific growth rates in their study of immature green turtles resident in the Bahamas. For comparative growth analysis specific growth rates have some advantages based on additive statistical properties and per unit measurement. On the other hand many studies are concerned with estimating a size-based growth function rather than summarizing size-specific growth in a single numeric measure and so absolute growth may be appropriate.

2.4.2 Age-based growth functions

The main purpose of growth studies when age is known has been to fit a parametric growth function useful for estimating important demographic processes such as maturation rate. The von Bertalanffy growth function has been widely used in sea turtle growth studies (see section 3). The age-based form of this function has no inflexion representing a monotone declining growth rate as the turtle ages through the post-natal development phase, irrespective of whether absolute or specific growth is used. Interestingly, of all the studies on sea turtle growth purporting von Bertalanffy growth only Bjørndal and Bolten (1988a) and Bolten et al. (1992) show a monotone declining size-specific growth rate and then only for part of the post-natal development phase.

The von Bertalanffy growth function has very poor statistical properties resulting in misleading and biased growth parameter estimates (Ratkowsky 1986). The same problems apply to the generalized von Bertalanffy or Chapman-Richards function (Ratkowsky 1990) used in a known-age growth study of West Atlantic immature green turtles (see Table 1). An even more generalized model known as the Richards function has been shown to have the worst statistical properties of any known function (Ratkowsky 1990). This function, also known as the generalized logistic or Richards-Nelder function, has not yet been used in sea turtle growth studies.

Ratkowsky (1990) has shown that other common parametric age-based growth functions used in sea turtle growth studies such as the logistic (Frazer and Schwartz 1984) and Gompertz (Caillouet et al. 1986) functions have excellent statistical properties. The sex-specific weibull functions used by Chaloupka and Limpus (1995a) also have good statistical properties (Ratkowsky 1990). Of course this applies so long as the function is fitted to data spanning the whole post-natal development phase.

Ratkowsky (1990) has shown that the statistical properties of many nonlinear parametric growth functions can be improved significantly by using expected-value parameters. This involves replacing some function parameters with known or fitted response variable values that correspond with say the lowest and highest known values of the explanatory variable. Say for instance that the response variable was curved carapace length (CCL) with known age (years) as the explanatory variable then initial estimates of suitable expected-values can be read from a nonparametric regression smooth of the bivariate data plot (see Cleveland 1993). The initial estimates would replace unknown parameters in a reparameterized form of the function being used. Recall that this concept of using biologically relevant values was also suggested for length-at-age back calculation procedures (see section 2.3.3).

Schnute and Fournier (1980) and Ratkowsky (1986) provide expected-value parameter forms of the von Bertalanffy function. All reparameterizations of the von Bertalanffy growth function have excellent statistical properties (Ratkowsky 1990). A point implicit in the expected-value approach is that growth functions are only fit to the range of observed data. Extrapolating any function beyond the empirical range is fraught with difficulties. This principle applies of course irrespective of the growth function used but has not been well adhered to in sea turtle growth studies (see section 3).

2.4.3 Mark-recapture analogues

It has been common practice to use mark-recapture or size-based analogues of the parametric growth functions when age is unknown, which is invariably the case with sea turtles. Mark-recapture analogues used are the absolute (Fabens 1965) and specific (Kaufman 1981) growth analogues of the von Bertalanffy growth function and the absolute growth analogue of the logistic growth function (Schoener and Schoener 1978). It is a simple task to derive these types of analogues for many other parametric growth functions.

These analogues have been used for two main purposes – (1) to derive growth parameter estimates from absolute or specific growth data sets provided from mark-recapture studies and (2) to substitute these parameter estimates into an analogous age-based growth function to generate a size-at-age function. There are two major problems with both practices.

Firstly, the poor statistical behaviour of the von Bertalanffy function has also been shown for the Fabens analogue (Chien and Condrey 1987, Francis 1988) and using similar arguments it follows that the logistic analogue (Schoener and Schoener 1978) would have poor properties. Francis (1988) gives an expected-value reparameterization of the Fabens analogue while Francis (1995) gives an analogue of a general growth

model (Schnute 1981), which can also be used in expected-value form. Bear in mind that these models provide growth-at-size functions not growth-at-age functions.

Secondly, the widely accepted practice in sea turtle studies of parameter substitution (see section 3.2.3.3) is inappropriate because size-based growth parameters are not equivalent to age-based growth parameters – they are analogous but not equivalent as clearly shown by Francis (1995). Put simply, replacing the growth parameters in say the von Bertalanffy age-based function with parameter estimates derived from either the Fabens or Kaufman size-based analogues is invalid. The same applies to use of all other analogues. The only apparent way around this problem when age is unknown is to use numerical integration to derived separate growth-at-size and growth-at-time-at-large functions. This could also be done using a Francis analogue but as discussed below analogues cannot take into account the confounded time-dependent nature of growth data unlike the statistical modelling and numerical integration approach of Chaloupka and Limpus (1995a).

Finally, a point relevant to statistical fitting of age- and size-based growth functions concerns goodness of fit. It is common practice in sea turtle growth studies using nonlinear regression to use R^2 as a numerical goodness of fit measure. This is a fallacious practice (Ratkowsky 1990 and references therein). Goodness of fit for nonlinear regression is a matter of judgment based on residual variance, examination of residuals and assessment of underlying assumptions.

3. Growth models

A wide selection of sea turtle growth studies have been arranged in Table 1 into one of twelve groups according to the following factors – (1) whether the main focus was on age or size, (2) the implicit sampling design (cross-sectional, longitudinal, mixed longitudinal) and (3) the specific analytical method used. Table 1 includes the citation, species, ontogenetic range, location, growth metric and underlying explicit or implicit growth behaviour. We discuss these twelve groups below but first of all we raise four major issues relevant to a critical review of all groups.

Firstly, sea turtle development undoubtedly comprises separate growth compartments representing distinct ontogenetic phases – Ricker (1975) refers to ontogenetic phases as growth stanzas. Just how many phases is unknown but at the very least there are distinct pre-natal and post-natal developmental phases. The number of phases within the post-natal period will depend on the ontogenetic habit of each species. For instance, the flatback (*Natator depressus*) has no epipelagic development phase but remains in a neritic habitat (Walker 1991). Notwithstanding individual growth variability, distinct developmental phases are most likely to have different somatic growth characteristics.

However, it has been a very common practice in sea turtle growth studies to fit a monophasic growth function to a limited ontogenetic range assuming that the chosen parametric function reflected the entire (rarely observed) post-natal development period. There is simply no substantive basis for such a practice. Most of the growth studies shown in Table 1 that fitted growth functions have done this, although some studies (Bjorndal and Bolten 1988a) have long recognized this as an inappropriate practice.

Secondly, another wide spread practice (Table 1) has been to discard multiple growth measurements per individual thereby turning implicit mixed longitudinal sampling into explicit mixed cross-sectional sampling (see section 2.1.2; Table 1 footnotes; also Fitzhugh 1975 for a discussion of data types). The usual approach has been to use only data from first capture and last recapture and discard recapture events (if any) in between. The same approach is prevalent in skeletochronological work where growth marks between the earliest and the last are disregarded in growth measurement for growth layer adjustment procedures.

There is no apparent basis for this practice other than perhaps a misunderstanding that repeated observations on some individuals and not others in a data set is invalid. It isn't and in fact mixed longitudinal sampling (sampling with partial replacement) has many desirable properties (Fitzhugh 1975, Berger 1986, Duncan and Kalton 1987, Skalski 1990) – so why throw away useful growth data?

Thirdly, a recurrent although not wide spread practice that is inappropriate in sea turtle growth studies is the discarding of zero or negative growth measurements prior to analysis. We can find no statistical basis for such a practice. Lastly, it must be borne in mind that many studies shown in Table 1 were based on mark-recapture programs using unreliable tag types and tagging protocols (see sections 2.2.2 and 2.2.3 above).

3.1 Age-based

The 18 studies classified as age-focused in Table 1 used either known age turtles or estimated age using skeletochronology (see section 2.3). All three sampling designs (cross-sectional, longitudinal, mixed longitudinal) were used reflecting the diversity of study settings and research purposes. If skeletochronology is coupled with back calculation (see section 2.3.3) then it is mixed longitudinal sampling, else it is cross-sectional sampling, which confounds age and cohort effects.

3.1.1 Cross-sectional

3.1.1.1 Known age

Ackerman (1981) studied embryonic growth in green turtles and loggerheads under a quasi-experimental field situation. Eggs were relocated from several West Atlantic beaches and incubated under beach conditions at the experimental sites. Eggs were sampled sacrificially over time from the relocated clutches to determine embryo growth (wet weight) for each stock and species. Sampling was cross-sectional assuming eggs were randomly sampled at each time both within and across the clutches otherwise there was additional uncontrolled error due to intra-clutch correlation. Logistic growth functions fitted the species-specific weight-at-age growth trajectories suggesting a nonmonotone age- or size-specific growth rate function. Growth of loggerhead and green turtle embryos slows prior to hatching, which is a characteristic growth behaviour known for producing precocial offspring (hatchlings) capable of surviving without parental care (Ackerman 1981).

3.1.1.2 Estimated age

The skeletochronological techniques developed by Zug and colleagues and Klinger and Musick (1992) for indirect age estimation reflects an important development in sea turtle growth studies (see section 2.3 for details).

The size-at-age growth functions generated by Klinger and Musick (1995) and Parham and Zug (1997) for warm temperate loggerhead stocks support age at maturity estimates derived from wild stock mark-recapture studies (Frazer and Ehrhart 1985, Frazer 1987, Frazer et al. 1994). Based on the skeletochronological and mark-recaptures studies mean age at sexual maturity for wild stock loggerheads seems to range between 25-35 years of age depending on the stock. The size-at-age growth function generated by Zug et al. (1996) for the Kemp's ridley suggests later age at maturity than estimates derived from captive reared (Caillouet et al. 1986) or headstarted mark-recapture studies (Caillouet et al. 1995). Zug et al. (1996) suggest that mean age at sexual maturity for wild Kemp's ridleys ranges between 11-16 years of age. Zug and Parham (1996) have recently derived leatherback age estimates using skeletochronological analysis of sclerotic ossicles. These are the first substantive growth records for wild stock leatherbacks. Bearing in mind the very small sample size Zug and Parham (1996)

suggest that mean age at sexual maturity in wild stock leatherbacks is around 13-14 years of age.

A problem with these studies relates to the von Bertalanffy growth function used. The growth function was fitted in all cases to a limited age-size range yet was used to represent the entire post-natal development period. This is not appropriate, especially if post-natal development is polyphasic. Whether the von Bertalanffy growth function is appropriate for sea turtle development is questionable and just about any function could fit such a narrow range of data – this may explain why several parametric functions are often found to provide a similar fit to the data. The von Bertalanffy function also has very poor statistical properties (see section 2.4.2).

Moreover, the von Bertalanffy function implies monotonic age- or size-specific growth rates for which no empirical support was provided. Zug et al. (1995) used skeletochronology to estimate age in loggerhead juveniles caught in the North Pacific high seas drift-net fishery. A von Bertalanffy growth function was also used to determine size-at-age and age-specific growth rates. Chaloupka (1996a unpublished) has reanalysed these data and found that growth was polyphasic and best fit using a nonlinear regression comprising the summation of two logistic functions reflecting growth spurts in the first year or so and then again around 5 years of age – simply plotting the data in Zug et al. (1995, Table 2) will reveal that growth was polyphasic and would be poorly fit by a von Bertalanffy function (see also growth records for pelagic loggerheads in Bjørndal et al. 1994). Irrespective of the analysis and the small sample size, this study (Zug et al. 1995) makes a significant contribution to understanding the epipelagic phase for loggerheads (see Bowen et al. 1995) and suggests that the pelagic phase for some stocks may well span 10 or more years.

Growth mark validation, growth layer loss correction and length back calculation are major problems for all skeletochronological studies and growth findings need to be considered cautiously (see section 2.3). Zug et al. (1996) employed an intriguing form of back calculation coupled with the Fabens size-based analogue of the von Bertalanffy growth function to generate an apparently age-free estimate of age-based growth. Substitution of size-based growth parameters say from the Fabens function into the conventional age-based von Bertalanffy function is invalid (see section 2.4.3).

Klinger and Musick (1995), Parham and Zug (1997) and Zug et al. (1996) found significant growth variability, which is attributable to natural variability in growth rates due to age, year and cohort effects. However, they also used growth record discarding so sampling was explicit mixed cross-sectional confounding age and cohort effects. The irony is that using back calculation properly (see section 2.3.3) they would have had mixed longitudinal sampling rather than cross-sectional. Skeletochronological age estimation coupled with length back calculation provides the best opportunity for undertaking age, year and cohort analysis of sea turtle growth rates (see sections 2.1.2 and 3.2.3.4), which could lead to new insights into sea turtle growth dynamics.

3.1.2 Longitudinal

Many sea turtle growth studies have been based on known age captive reared turtles (Table 1). Such studies involve longitudinal sampling, which confounds age and year effects on growth rates. This is not a major issue if the year effect is irrelevant say in a controlled experiment to study dietary effects on growth (Phasuk and Rongmuangsart 1973, Davenport and Scott 1993). Due to space constraints we won't consider the large number of these sorts of captivity based growth experiments but foreshadow that a critical review is warranted.

A number of compilations of captive reared growth information are available (eg., Zug et al. 1986, Godínez-Domínguez et al. 1993). The main insight is that all species develop much faster under various captive conditions than is apparent in wild stocks. It

is apparent that growth variability of a study cohort increases with age even under captive conditions suggesting significant individual variability in age to sexual maturity.

Several studies (Witzell 1989, Marquez 1972, Caillouet et al. 1986) fitted parametric growth functions to estimate growth rates and mean age to maturity. Marquez (1972) fitted a von Bertalanffy function to Kemp's ridley growth data, implying monotone decreasing size-specific growth rates. On the other hand Caillouet et al. (1986) used a Gompertz model for Kemp's ridley implying nonmonotone size-specific growth rates. The Gompertz function has excellent statistical properties and the von Bertalanffy function has poor properties (Ratkowsky 1990). Recall that Zug et al. (1996) also fitted a von Bertalanffy function to estimated age at size data for wild stock Kemp's ridleys. All three studies fitted functions to incomplete ontogenetic ranges. Whether this species has nonmonotone size-specific growth is therefore unresolved. Moreover, Marquez's (1972) data included a mix of captive and mark-recapture growth records.

While longitudinal designs confound age and year effects, cohort effects are not necessarily effected. For instance, Caillouet et al. (1986) found strong cohort (year class) effects in a study of Kemp's ridley growth in captivity. It is noteworthy that the mean growth function for an initial study cohort of about 20 olive ridleys (Phasuk and Rongmuangsart 1973) shows seasonal growth. Neither Phasuk and Rongmuangsart 1973 nor Mohanty-Hejmadi 1992 fitted size-at-age functions to their olive ridley growth data but it is clear from graphical presentations in both studies that age-specific growth rates were nonmonotonic.

Uchida (1967) and Frazer and Schwartz (1984) fitted the logistic function to the growth profiles of individual loggerheads, suggesting nonmonotone size-specific growth. The logistic function in most parameter forms has excellent statistical properties (Ratkowsky 1990). Both studies fitted functions to incomplete ontogenetic ranges. The two loggerheads reared under controlled captive conditions (Uchida 1967) grew 2-3 times faster than the two loggerheads reared under semi-natural captive conditions (Frazer and Schwartz 1984). The difference was attributed to experimental settings related to temperature and food treatments (Frazer and Schwartz 1984). The difference in experimental setting reinforces the confounding of age and year effects inherent in longitudinal studies. Under controlled experimental conditions (Uchida 1967) the confounded year effect will be masked. But in semi-natural experiments spanning nearly 14 years like Frazer and Schwartz (1984) then the confounding of age and year effects will not be masked if year effects occur. This might be the case in Frazer and Schwartz (1984) where the individual profiles display irregular monophasic logistic growth behaviour more suggestive of polyphasic logistic growth.

We caution against using captive reared growth information for drawing conclusions about growth dynamics of wild stock sea turtles. Longitudinal growth studies confound age and year effects, irrespective of whether controlled experimental or semi-natural rearing conditions were used. Moreover, some captive study designs are questionable variations of conventional sampling design. Of particular note is Witzell (1980) who fitted a von Bertalanffy function to hawksbill size-at-age data and inexplicably censored all data prior to 53 weeks of age. The sampling design was also extremely complex starting as cross-sectional for the first 18 weeks, then at 32 weeks it became longitudinal when six selected turtles were followed to 84 weeks and then two selected turtles were followed until study end at 128 weeks.

3.1.3 Mixed longitudinal

3.1.3.1 Known age (headstarted stock)

Although assigned to a mixed longitudinal group both studies (Ehrhardt and Witham 1992), Caillouet et al. 1995) used explicit mixed cross-sectional sampling. Caillouet et al. (1995) used growth record discarding while Ehrhardt and Witham (1992) had

insufficient recaptures per individual at the time of the study. Therefore age and cohort effects are confounded in both studies. Caillouet et al. (1995) fitted the von Bertalanffy function to Kemp's ridley data implying monotonic size- or age-specific growth rate functions (cf. Caillouet et al. 1986 implying nonmonotonic growth rates in captivity). Ehrhardt and Witham (1992) fitted the generalized von Bertalanffy function to green turtle data implying nonmonotonic size- or age-specific growth rate functions. Both the standard and generalized von Bertalanffy functions have poor statistical properties (see section 2.4.2) and, moreover, both functions were fitted to limited data ranges.

Ehrhardt and Witham (1992) made no mention of tagging nor provided standard errors for fitted parameters making it difficult to assess data reliability or model adequacy. Irrespective of these concerns the empirical growth pattern for the ontogenetic range observed in their study was asymmetric implying nonmonotone size- and age-specific growth rate functions. Ehrhardt and Witham (1992) provided a time derivative of the estimated size-at-age function to derive the age-specific growth rate function. The age-specific growth rate function for this headstarted green turtle stock displayed increasing growth from hatching to about 10 years of age then slowly decreasing to sexual maturity. Ehrhardt and Witham (1992) used the Chapman-Richards (generalized von Bertalanffy) growth function, which is asymmetric about the inflexion rather than skew-symmetric such as the logistic. If an asymmetric function is needed then the Gompertz or an expected-value reparameterization of the Chapman-Richards function (Ratkowsky 1990) might be appropriate. The weibull-type growth function (Chaloupka and Limpus 1995a; see section 3.2.3.4) is also a flexible asymmetric parametric function with good statistical properties (Ratkowsky 1990).

The value of headstarted growth studies is questionable since growth rates were accelerated at a critical ontogenetic phase with unknown consequences, an issue acknowledged by Caillouet et al. (1995). Nonetheless, headstarted studies are more informative than captive reared studies and cannot be discounted until a wide range of reliable wild stock studies have been carried out – which is not the case at present.

3.1.3.2 Known age (wild stock)

Since 1976 around 130,000 loggerhead and 109,000 green turtle hatchlings have been marked with a mutilation tagging protocol in the southern Great Barrier Reef region (Limpus et al. 1994a,b). One immature female loggerhead (15.2 years, 75.6cm CCL), one immature female green turtle (8.75 years, 54.4cm CCL) and one immature green turtle male (11.25 years, 68cm CCL) have now been recovered in a warm temperature foraging area well south of the southern Great Barrier Reef rookeries (Limpus et al. 1994a,b). Assuming that tag recognition is reliable, these data are invaluable although insufficient at this stage to be of substantive use for modelling growth dynamics. Other long-term tagging and monitoring programs will undoubtedly also begin soon to provide known age wild stock recoveries.

3.2 Size-based

The 21 studies classified as size-focused in Table 1 used either known age turtles (captive reared, headstarted) or age was unknown. In most cases the purpose of the study was to investigate growth rates although many also had the explicit intention of determining a size-at-age function from length data. All three sampling designs (cross-sectional, longitudinal, mixed longitudinal) were used reflecting the diversity of study settings and research purposes. Only three studies (Bolten et al. 1992, Chaloupka and Limpus 1995a, Chaloupka and Limpus 1996a) have taken a statistical approach to better understand growth dynamics. Two studies (Chaloupka and Limpus 1995a, Chaloupka and Limpus 1996a) have attempted to take into account the confounded time effects of time sampled growth information.

3.2.1 Cross-sectional

3.2.1.1 Length frequency

Although the main focus of the following studies was to estimate an age-size function rather than growth rates they are nonetheless size-based models. The sampling is cross-sectional so age and cohort time effects are confounded. Length frequency analysis assumes that a length frequency distribution will comprise a series of distinct modes or pseudo-cohorts corresponding to specific age classes. The lengths in each age class are assumed to have a parametric distribution around their mean length (usually Gaussian) and be of equal variance. The mean lengths at age are also assumed to lie along a parametric growth function – usually assumed to be a von Bertalanffy growth function.

Le Toquin et al. (1980) used single sample length-frequency analysis to estimate size-at-age functions for an Indian Ocean immature green turtle stock. The sample was too small, spanned an inadequate ontogenetic range and the technique for mode detection was inappropriate. Single sample length frequency analysis is discussed in Ricker 1975. While not assigned to this group, it is worth mentioning that Frazer (1987) used the Fabens analogue to convert a single sample length frequency distribution to derive an age frequency distribution (see section 3.2.3.3, size-based analogues).

Bjorndal et al. (1995) used sequential sample length-frequency analysis (Fournier et al. 1990) to estimate growth and age-size functions for an immature green turtle stock resident in southern Bahamas. They compared the estimated growth parameters with growth interval and Fabens analogue growth parameters derived from a mark-recapture program. Bjorndal et al. (1995) concluded from their length frequency analysis that it takes the immature turtles at this site about 12 years to grow from recruitment (ca. 25 cm SCL) to 70 cm SCL when they disperse to other habitats.

The Bjorndal et al. (1995) comparative study presents an interesting dilemma since the length frequency analysis was based on cross-sectional sampling (age and cohort confounded) whereas the growth interval and the Fabens function were based on mixed longitudinal sampling of unknown age (year and cohort confounded). Based on statistical sampling considerations alone it seems that the approaches are incomparable. Moreover, without an independent and corroborative source of age only a weak form of inference was logically possible. Also the study assumed that growth for this stock was represented by a von Bertalanffy function implying monotonic size- and age-specific growth rates for the entire post-natal development phase. There was no empirical basis to this assumption.

Sequential length frequency analysis using say MULTIFAN (Fournier et al. 1990) is not just a growth function it is in fact a sophisticated modelling system. Therefore it should come as no surprise that it is one of the most assumption laden parametric approaches to growth modelling. Modelling length frequencies or age frequencies for that matter without auxiliary biological information is a notoriously difficult task. Therefore length frequency methods need constraints imposed on the von Bertalanffy growth function parameters being estimated otherwise the model is not estimable.

Imposing biologically reasonable constraints is not a simple task and is quite subjective (Fournier et al. 1990). Yet the main advantage claimed for length frequency analysis is it doesn't need expensive mark-recapture programs. It is ironic then that the approach depends on inclusion of demographic information to provide the model constraints that can only be obtained by a mark-recapture program in the first place. Other more recent length frequency modelling approaches based on artificial intelligence algorithms depend even more on incorporating reasonable biological constraints (see Golikov et al. 1995). We reserve our judgment on the utility of the length frequency approach, irrespective of the modelling approach used.

3.2.1.2 Parametric growth rate model

Bolten et al. (1992) were the first to adopt a statistical modelling approach to analysing growth rate information for sea turtles. They derived size-specific absolute growth rates for 88 immature green turtles in a developmental habitat in the Bahamas. The size-specific growth function was monotone decreasing. Sex was determined for each turtle using radioimmunoassay. Using a linear regression model Bolten et al. (1992) found no sex-specific difference in the size-specific growth rates for this stock, at least not for the range of sizes in the study (ca. 32-60cm SCL). The sampling design was cross-sectional because it was a one-off study and because of growth record discarding confounding age and cohort time effects. Age was unknown so year and cohort are also confounded. Since growth was the focus not age then age/cohort confounding is not important. On the other hand, year and cohort effects are important, especially since the site is a developmental habitat, which would be subject to highly variable annual recruitment and growth (see Bjorndal et al. 1995).

3.2.2 Longitudinal

Swingle et al. (1993) provide weekly growth records for twelve conspecific captive reared loggerheads monitored for two years at several different sites. These data reflect longitudinal sampling hence age and year effects are confounded making conclusions about wild stocks questionable. Age was known but the focus was growth rates rather than age. The weekly growth profiles enable investigation of potential seasonal growth and perhaps polyphasic growth similar to the study on captive reared olive ridleys discussed above (Phasuk and Rongmuangart 1973; see section 3.1.2).

3.2.3 Mixed longitudinal

3.2.3.1 Known age (headstarted stock)

Age was known but the authors (Kowarsky and Capelle 1979, Wood and Wood 1993, Bjorndal and Bolten 1988b) focused on growth rather than age. These studies used longitudinal sampling hence age and year effects are confounded making conclusions about wild stock growth rates questionable. Sample sizes were also extremely small for two studies – twelve green and two hawksbill recoveries by Kowarsky and Capelle (1979) and five recoveries from three loggerheads (Bjorndal and Bolten 1988b). Monotonic size-specific growth was inferred by Bjorndal and Bolten (1988b) for a loggerhead stock in the Bahamas but there was no empirical basis for this view.

Since 1980 around 27,000 green turtle hatchlings and yearlings have been marked with autografts and mutilation tags for hatchlings and single plastic or titanium tags for yearlings and released around the Cayman Islands (Wood and Wood 1993). A number of recaptures have occurred providing information on headstarted growth rates, local dispersal and incidence of fibropapillomas. As already mentioned, the value of headstarted growth studies is questionable.

3.2.3.2 Growth interval

Besides the captive reared growth studies, this group reflects the bulk of sea turtle growth studies. This is not surprising given that many studies were motivated by the apparent disparity between growth information obtained from captive reared turtles and data obtained from wild stock observations.

Sampling design was mixed longitudinal (but age unknown) except for Collazo et al. (1992), Green (1993) and Boulon (1994) where it was explicit mixed cross-sectional due to growth record discarding thereby confounding age and cohort effects. As already mentioned, growth record discarding is an unnecessary practice. For all studies the year and cohort effects are confounded because age was unknown. Most studies

used multiple monel tagging protocols (see section 2.2.2) except for Balazs (1982, inconel tags), Limpus (1992b, titanium tags) and Bjorndal et al. (1994, plastic tags). Most studies only covered a limited ontogenetic range and provided small sample sizes.

The basic method is the compilation of mark-recapture growth records over time. Then mean annual absolute growth rates are calculated and grouped into 5 or 10 cm size increments referenced either to mean size or initial size at first capture to indicate size-specific growth. The approach is simple and has been the basis for useful comparative analyses across a broad geographic range (see Bjorndal and Bolten 1988a, Limpus 1992b, Green 1993). Several studies (Limpus and Walter 1980, Collazo et al. 1992, Limpus 1992b, Green 1993, Bjorndal et al. 1994) found nonmonotonic size-specific growth patterns for green turtles, loggerheads and hawksbills from several different geographic locations. Nonmonotonic size-specific growth implies asymmetric (e.g., Gompertz type) or skew-symmetric (e.g., logistic type) size-at-age functions. Three studies (Bjorndal and Bolten 1988a, Mendonca 1981, Boulon 1994, see also Bjorndal et al. 1995) found monotonic size-specific growth for green turtles, loggerheads and hawksbills from western Atlantic-Caribbean locations. Monotonic size-specific growth implies a noninflexion asymptotic size-at-age function (e.g., von Bertalanffy type).

The growth interval approach is useful but limited because the grouping arrangement precludes application of individual covariate information essential for any further statistical modelling (cf. Limpus 1992b and Chaloupka and Limpus 1996a unpublished discussed in section 3.2.3.4 below).

3.2.3.3 Size-based growth analogues

Bjorndal and Bolten (1988a) used the Kaufman size-based analogue of the von Bertalanffy growth function to study specific growth in an immature green turtle stock in the Bahamas. The main focus of this study was growth not age. The sampling design was mixed longitudinal but as age was unknown, year and cohort effects are confounded. They used the Kaufman (1981) approach to determine if the size-specific growth data implied either logistic, von Bertalanffy or Gompertz type size-at-age growth – growth was specific not absolute growth. The Kaufman approach precluded the need to specify unknown growth parameters such as mean adult size. They found that von Bertalanffy growth behaviour best reflected the size-specific growth pattern for the recorded size range. The empirical size-specific growth function was monotone decreasing for the recorded size range (25-70cm SCL). But the Kaufman analogue is inappropriate for two reasons – (1) it isn't applicable for estimating von Bertalanffy parameters anyway (see Kaufman 1981) and (2) replacing parameters in age-based functions with parameters from size-based analogues is invalid (see section 2.4.3), although this latter use was intentionally avoided by Bjorndal and Bolton (1988a).

The Bjorndal and Bolten (1988a) study has been extended by Bjorndal et al. (1995) in a comparison of sequential length frequency analysis, growth interval method and Fabens analogue of the von Bertalanffy growth function (see also section 3.2.1.1). This time the main focus was age but the method was still size-based. They used the Fabens analogue to derive a size-at-age function fitted only to the observed size range. The Fabens size-based analogue has known poor statistical properties (Chien and Condrey 1987) and, moreover, using any size-based analogue to provide age-based parameter estimates for the von Bertalanffy growth function is invalid (Francis 1995 and references therein; see section 2.4.3). Nonetheless, it appears the empirical size-specific growth function for this 25-70cm SCL green turtle stock (Bjorndal and Bolten 1988a, Bjorndal et al. 1995) does display monotone decreasing size-specific growth rates unlike say for in the southern Great Barrier Reef region (see Chaloupka and Limpus 1995a, section 3.2.3.4).

The main focus of Frazer and Ehrhart (1985), Boulon and Frazer (1990) and Frazer et al. (1994) was on deriving size-at-age functions for green turtles and loggerheads from

mark-recapture length data. In fact, the growth function derived by Frazer et al. (1994) was used to form the age-structure of a loggerhead population model (Heppell et al. 1996), which we discuss below (see section 5.2.2). Recall also that Zug et al. (1996) used the Fabens analogue to derive a size-at-age function for age-estimated Kemp's ridley in a mixed cross-sectional study (see section 3.1.1.2).

The sampling design for these four studies should be mixed longitudinal but because of growth record discarding it was explicit mixed cross-sectional with age and cohort effects confounded. All four studies fitted von Bertalanffy type growth functions to a limited ontogenetic range assuming that the function reflected the entire unobserved post-natal development period. This is simply not appropriate. All four studies used the Fabens size-based analogue approach to derive age-based growth parameters to substitute into the von Bertalanffy age-based growth function. As already mentioned this approach is invalid (Francis 1995 and references therein; see section 2.4.3).

Frazer and Ehrhart's (1985) study was extended by Frazer (1987) using the Fabens analogue to back transform a length frequency distribution for stranded loggerheads to derive an age frequency distribution (catch curve) for estimating age-specific survival. The same issues remained unresolved. We discussed elsewhere (see section 2.4.3) suitable approaches to size-based growth studies and size-based analogues.

All seven studies discussed here concluded that somatic growth was best expressed as a von Bertalanffy growth function implying monotonic size- and age-specific growth rate patterns. Excluding Bjorndal and Bolten (1988a) the remaining six studies concluded that the von Bertalanffy function reflected growth for the entire post-natal development phase, which was highly questionable since no study had sufficient data range and the latter six studies used inappropriate size-based analogues to derive such a conclusion.

3.2.3.4 Nonparametric growth rate models

Chaloupka and Limpus (1995a) developed size-, sex- and age-specific somatic growth rate models for the southern Great Barrier Reef (sGBR) green turtle stock using a large data set derived from a long-term mark-recapture program (see Limpus 1992b). Tagging used the multiple titanium tagging protocol and the sampling design was mixed longitudinal (≥ 1 measurements per individual) with data spanning the entire post-pelagic developmental phase.

They modelled absolute growth rate as a function of informative covariates such as size (CCL), sex and recapture interval using nonparametric regression modelling known as generalized additive modelling (Hastie and Tibshirani 1987). They found nonmonotone size-specific growth rates that increased from recruitment size (>35 cm) to maximum growth rate around 60-65 cm CCL and then decreasing slowly to about 100 cm CCL. Female growth was significantly different from male growth diverging at about 60 cm CCL. They found significant inter-annual variation in female growth rates.

Using numerical integration of B-splines they derived size to time-at-large growth functions for each sex from the size-specific growth functions. Their empirical solution models suggest that both females and males in the sGBR green turtle stock must be ≥ 30 -35 years-at-large before reaching sexual maturity. Time-specific growth functions for each sex were also provided suggesting maximum growth for females occurs at 10 years-at-large (60cm CCL) and at 12 years-at-large (63 cm CCL) for males. The size to time-at-large functions were modelled using simultaneous nonlinear equations to provide analytical solutions to the mean size to time-at-large growth curve for each sex. These weibull-type functions have good statistical properties (Ratkowsky 1990) and fitted the numerically integrated growth data well.

A generalized additive modelling approach was also used by Chaloupka and Limpus (1996a unpublished) to analyse absolute growth rates for a sGBR hawksbill stock (see

Limpus 1992b). Sampling was mixed longitudinal (≥ 1 measurements per individual) with data spanning the entire post-pelagic developmental phase. They found a nonmonotone size-specific growth function and strong year effects but the data set was too small to adequately differentiate sex dependent growth.

The nonparametric statistical modelling approach developed by Chaloupka and Limpus (1995a) has many useful features including – (1) the data determine the underlying growth function rather than using a parametric function that bears little resemblance to the data and (2) the growth data are conditioned on informative covariates to support a better understanding of the growth process itself. There is a price, however – it is more complex. Moreover, year and cohort effects were confounded in both this study and Chaloupka and Limpus (1996a unpublished) because age was unknown despite the sampling designs being mixed longitudinal.

4. Comparative Life History Patterns

4.1 Comparative life history traits

There are three common schemes for interpreting life history strategies – (1) deterministic r-K theory (Stearns 1976), (2) stochastic bet-hedging theory (Stearns 1976) or (3) age-specific reproduction axioms focusing on residual reproductive value (see Zammuto 1987). The schemes are all special cases of a more general demographic classification of environmental setting or habitat. The study of growth dynamics focuses on demographic implications of ontogeny while life history theories focus on demographic implications of phylogeny. The demographic implications of the interaction between growth, life history and environment forms the basis for population dynamics and macroevolutionary change.

The r-K theory assumes density independence and environmental invariance and has been coopted to support various linear deterministic growth, population and macroevolutionary theories. However, variability in timing of maturation and growth (Alberch et al. 1979) and environmental stochasticity (Tuljapurkar 1990) seem more likely to be the keys to unlocking complex life history patterns.

Nevertheless, the most common framework apparent in sea turtle research is the r-K theory. For instance, r-K theory is implicit in all deterministic models shown in Table 2. In fact it is explicit in the life table schedules (Frazer 1983, 1984, 1986) and the matrix projection models of Crouse et al. 1987, Laurent et al. 1992, Crowder et al. 1994, Somers 1994 and Heppell et al. 1996. Interestingly, there are no tests of life history theories using sea turtle growth, population or macroevolutionary patterns.

Two approaches that could be adopted for such a study are – (1) a prospective approach based on stochastic simulations (eg., see section 5.3.1; Chaloupka and Limpus 1995b) to test demographic forecasts of competing life history theories on the temporal behaviour of a hypothetical population and (2) a retrospective approach based on comparative analysis of life history patterns recorded from various environmental settings. The two approaches are not necessarily mutually exclusive. The prospective approach has not been used in sea turtle research while important qualitative progress has been made using comparative analysis of static life history traits.

Van Buskirk and Crowder (1994) produced a compendium of selected life history traits for 96 stocks of the seven extant sea turtle species enabling analysis of both inter-generic and intra-specific covariation. They used these data for an analysis of inter-generic life history covariation based on a combination of correlation and linear regression derived residuals to control for size. Given the nonorthogonal hierarchical nature of such data sets it might be worthwhile in future to consider the use of classification trees (Breiman et al. 1984) or visualization tools such as coplots

(Cleveland 1993) for exploring the relationship between size, phylogeny and life history patterns. Despite the limited and incomplete data set and limited methodology they nonetheless were able to draw several broad qualitative conclusions.

Perhaps the most important conclusion disregarding adult body size was that the seven extant species of sea turtles could be readily classified into two distinct groups based on mean fecundity and neonate characteristics – group 1 comprised leatherbacks and flatbacks with smaller clutch size, larger egg volume and larger hatchling size while group 2 comprised greens, loggerheads, hawksbills and both ridleys with larger clutch size, smaller egg volume and smaller hatchling size. It may be no coincidence that both group 1 species (leatherbacks, flatbacks) also have similar adult gait, egg laying posture and adult carapacial skin (Limpus et al. 1988).

While not stated in van Buskirk and Crowder (1994) these two groups represent distinct ontogenetic patterns. Group 1 species live in one general habitat irrespective of ontogeny – flatbacks remain neritic with no pelagic phase (Walker 1991) while leatherbacks remain pelagic except of course when nesting. On the other hand group 2 species have a distinct post-natal pelagic phase proceeded years later by recruitment to a neritic immature-adult phase. The transition from pelagic to neritic habitat represents a major ontogenetic shift and is one of the many reasons why a single growth function is inappropriate for representing post-natal growth of at least group 2 species where growth is clearly polyphasic (see section 3.1.1.2).

Another possibility regarding these two ontogenetic groups is that they might well reflect two distinct phyletic groups based on pedomorphic heterochrony (see Alberch et al. 1979). Rhodin et al. (1981) consider that the leatherback skeletal morphology reflects neoteny, which is pedomorphism due to somatic retardation. Neoteny results from an ontogeny with a longer exposure to high juvenile growth rates leading to a morphologically retarded adult. It is interesting then that leatherbacks appear to have by far the highest juvenile growth rates of all sea turtle species reaching sexual maturity on average in around 13-14 years (Zug and Parham 1996).

Whether flatbacks are a macroevolutionary product of neotenic heterochrony like the leatherback is not known although flatbacks do retain a number of juvenile features in adulthood such as carnivory and poorly keratinized skin and scales (Limpus et al. 1988, Parmenter 1993). If they are neotenic then we would expect flatbacks to also have higher growth rates, which is feasible given that they are restricted to a continental shelf habitat with feeding grounds in shallow turbid inshore waters (Limpus et al. 1983b). If higher growth rates occur then perhaps earlier maturation rates offsets the impact of lower fecundity (Buskirk and Crowder 1994) on flatback population dynamics – else lower fecundity could be offset by higher hatchling and juvenile survival rates but we just don't know. And therein lies a consequence of the complex nature of sea turtle life history, growth and population dynamics – a litany of unresolved "if-then-else-but" statements.

There are insufficient comparative studies of sea turtle ecology, reproduction, embryology, morphology and somatic growth to support further insight into life history patterns. Comprehensive studies of growth dynamics and population dynamics across a range of environmental settings are needed to understand the complex relationship between sea turtle ontogeny, phylogeny and macroevolutionary change.

4.2 Comparative demography

Most sea turtles have an overlapping iteroparous life cycle – long life expectancy coupled with discrete multiple breeding seasons and overlapping generations. The nesting season is usually in summer but a northern Australian flatback stock (*Natator depressus*) has a winter nesting season (Guinea 1994). Several stocks have also been

shown to nest year round and so have a continuous iteroparous life cycle (eg., Sarawak greens, Hendrickson 1958; Crab Island flatbacks, Limpus et al. 1983a).

Comparison of limited growth interval profiles for some stocks indicated inter-regional differences in size-specific growth (Bjorndal and Bolten 1988a, Limpus 1992b, Green 1993) and mean adult size (van Buskirk and Crowder 1994) for green turtles and loggerheads. A difference in benthic phase recruitment size is also apparent between the Caribbean and the sGBR regions for green turtles, loggerheads and hawksbills. In the Caribbean region greens recruit at 20-25cm SCL, loggerheads at 40-45cm SCL and hawksbills at 15-25cm SCL (National Research Council 1990). On the other hand, in the sGBR region greens recruit at 35-40cm CCL, loggerheads at 68cm CCL and hawksbills at 40cm CCL (Limpus et al. 1994a, Frazer et al. 1994, Limpus 1992b respectively). Even accounting for transformation of SCL to CCL the recruitment size differences between regions and between loggerheads and the other species are considerable. Clearly there are common and yet local or regional patterns in sea turtle demography suggesting that there is sufficient phenotypic variability to warrant comparative demographic analyses to complement life history analyses.

Zug et al (1986) summarized captive and wild stock growth rates and estimated age at sexual maturity from many sources but these data are of limited value for comparative purposes. Important static survival (Fraser 1983, 1986) and fecundity (Frazer 1984) schedules have been derived for a loggerhead nesting stock (Little Cumberland Island, Georgia). Comparison of these life schedules with similar schedules derived for other loggerhead stocks would form the basis for a comparative demography but there seem to be few age-specific or size-specific survival or fecundity schedules available.

Bjorndal (1980) presented both cohort and relative age-specific survivorship data for a green turtle stock nesting at Tortuguero, Costa Rica. Chaloupka (1996b unpublished) has used a statistical model to account for the main effects of age, year and cohort in a reanalysis of Bjorndal's (1980) data. This modelling approach based on a generalized linear model with extra-poisson sampling variation (see McCullagh and Nelder 1985) provides an age-specific hazard function conditioned on the time-dependent effects (age, year, cohort). This time-conditioned hazard function would be suitable for inter-stock comparison if other such hazard functions were available.

Despite these studies there are no comparative analyses of intra- and inter-specific demography based on key attributes such as age- or size-specific mortality (hazard), fecundity, somatic growth or recruitment. It is certainly more difficult to compare demographic functions than static life history traits based on say mean fecundity or relative reproductive value. Nonetheless, important insights into demography and population dynamics will arise when such analyses are undertaken. To encourage such an analysis, which would need to be a collaborative research effort, we outline a standard modelling procedure that might be suitable for comparative demographic analysis based on somatic growth dynamics and mortality.

Firstly, a statistical analysis of age-specific growth if age known or else size-specific growth rates conditioned on time-dependent effects (year, cohort) is needed to estimate the growth function. If the estimated growth function is size-specific then numerical integration is needed to transform the function into age-specific form. Then a suitable parametric growth function could be fitted to the conditioned size-at-age data derived from either the age-specific or size specific forms. The weibull type nonlinear equation is useful here for comparative purposes, especially when used as a system of nonlinear simultaneous equation (Chaloupka and Limpus 1995a). The single equation form is –

$$y = \alpha - \beta \exp[-\exp(-\gamma)t^{\delta}] \dots\dots\dots (1)$$

where: y = size (length, weight)
 t = time (age or year-at-large)
 α = asymptote
 β = asymptote - y intercept
 γ = growth coefficient
 δ = dimensionless shape parameter

If the shape parameter $\delta=1$ then the growth function is an asymptotic regression function indicating monotone decreasing size-specific growth rates – a von Bertalanffy type function. The shape parameter enables the equation to fit either skew-symmetric or asymmetric functions. This model is the only flexible shape equation with known good statistical properties and expected-value forms are available (Ratkowsky 1990). It is easy to derive a size-based analogue of this function but its utility is questionable since it is our claim that all time-dependent demographic data needs to account for the age, year and cohort effects first.

For statistical estimation equation (1) or a system of equations (1) will include an error term, which can be autoregressive or moving average to account for n th order autocorrelation. In a system of equations the parameters can be either unique to each equation or common across equations as can the autocorrelation parameters. The system of equations is then best estimated using nonlinear SUR (Judge et al. 1984).

The weibull type model would then provide estimates of growth dynamics from several stocks expressed in summary form as (1) mean mature adult size (α), (2) growth coefficient (γ) and (3) the intrinsic growth function shape parameter (δ). These three parameters coupled with estimated mean age at sexual maturity would then provide a quantitative basis for inter-stock demographic comparison. These four key parameters could be derived also as sex-specific functions using the same process. The weibull type modelling procedure presented could also be applied to survivorship data for inter-stock comparative analysis. The advantage of using one reliable growth function such as equation (1) for comparing all stocks (sex, geographic, species) is that it would enable comparison of growth functions among the stocks in terms of the same growth parameters and estimates of standard errors.

Such a form of comparative demography based on growth and survivorship would complement well conventional life history analysis such as van Buskirk and Crowder (1994). The problem with just analysis of life history traits is that phenotypic variability of traits such as reproductive output is only epigenetic and of low heritability whereas somatic growth rates while environmentally influenced have high heritability. Moreover, growth dynamics is a fundamental aspect of macroevolutionary change (Alberch et al. 1979). Combining comparative demography and comparative life history would provide better insights into population dynamics. Major challenges exist in undertaking the modelling procedure related to lack of sufficient time-structured growth and survivorship data sets spanning the entire post-pelagic developmental phase.

5. Population Dynamics

A population is a set of individuals with a common life cycle, which is a sequence of morphological states structured by age and/or developmental stages. Population dynamics is about the analysis of temporal change in abundance and spatial structure to explore how a population responds to natural and human-induced perturbations. The abundance of individuals over time in each state is determined by five demographic processes or rates (birth, death, growth, immigration, emigration) subject to varying levels of environmental, demographic and genetic stochasticity.

The challenge for population dynamics is to integrate existing knowledge about specific life cycles with the demographic processes. Usually this involves mathematical

modelling of the spatio-temporal behaviour of the states as some function of the demographic rates – the rates may be time varying. Population dynamic models are useful for helping to provide insight into the complex mechanisms affecting temporal and spatial change in population abundance on a scale not amenable to experimental control or observation.

Sea turtle demographic analysis and population modelling is very much in its infancy. All known sea turtle population models have been arranged in Table 2 into one of five groups according to the following factors – (1) model type as either *i*-state distribution or *i*-state configuration (see DeAngelis et al. 1993), (2) whether model was deterministic or stochastic (see Getz and Haight 1989), (3) whether model was static (steady state) or dynamic and (4) whether the demographic structure was age or stage classified (see Manly 1990, McDonald and Caswell 1993). Table 2 includes the citation, species, specific modelling approach, location and model purpose. The distinction between *i*-state distribution and configuration models was included to place sea turtle models in a broader modelling context since so-called individual-based models (IBMs, *i*-state configuration) are emerging in other fields.

The distinction between static and dynamic is a bit arbitrary since only the difference equation models of Chaloupka and Limpus (1995b, 1996b unpublished) are really dynamic where the demographic processes are time varying and involve feedback mechanisms. Many authors such as Getz and Haight (1989) consider models to be dynamic when a model has a potential capacity for modeling so-called transient and time-dependent behaviour. This is in fact a rather liberal definition of dynamic since all deterministic models in Table 2 (sequential population, life table, dynamic pool, matrix projections) are in fact all related to a generalized matrix model (Getz and Haight 1989) which is itself a special case of generalized difference equation modelling frameworks.

5.1 Deterministic age structured

All the deterministic models in Table 2 are based on a deterministic and linear theory of population growth where demographic rates are assumed to be density independent and stationary (time invariant) resulting in a stable age distribution (Keyfitz 1985). In other words demographic rates are assumed to be time-independent thereby confounding age, year and cohort effects. One implication being that individuals are assumed to develop at the same rate and so reach sexual maturity at the same age. These assumptions are expressed as knife-edge recruitment in the Marquez M et al. (1982a,b) models.

5.1.1 Static age-structured

All models assigned here (Marquez M et al 1982a,b, Richardson and Richardson 1982; Frazer 1983, 1984, 1986) are some form of age-structured life table model (a life table could of course be size- or life-state structured).

Marquez M et al. (1982a,b) developed population models for hypothetical populations of olive and Kemp's ridleys based on demographic information related to stocks nesting along the Mexican coast. Both models are based on a variant of sequential population analysis (SPA) common in fisheries stock assessment (see Megrey and Wespestad 1988). SPA is a deterministic method based on many assumptions including constant annual recruitment independent of the spawning stock and both a growth function and constant hazard function that are age and year invariant. The demographic information available at the time the model was developed was limited. They determined female mortality rates from a mark-recapture program and assumed both species reached sexual maturity between 7-8 years of age. Zug et al. (1996; see Table 1) suggest that mean age at sexual maturity for wild Kemp's ridley ranges between 11-16 years of age. Marquez M et al. (1982a,b) used their SPA variant to derive hindcast age-cohort stock estimates. SPA is a derivative of virtual population (VPA) or cohort analysis (Megrey and Wespestad 1988). SPA has all the same assumptions as VPA

except that the hazard function implicit in Marquez M et al. (1982a,b) comprises natural mortality but no fishing related mortality. While not immediately obvious, SPA is also closely related to age-structured matrix models (Getz and Haight 1989).

Richardson and Richardson (1982) developed a simulation model for a hypothetical cohort to reflect the loggerhead nesting stock dynamics at Little Cumberland Island, Georgia (USA). The model is best described as a life table with a stock-recruitment function based on the product of relative age-specific fecundity and mortality schedules. It incorporated 5 or 10 year cyclical patterns in fecundity to simulate cyclical patterns in stock abundance reflective of the observed nesting stock at Little Cumberland Island. Frazer (1983, 1984, 1986) derived static life table schedules for the same loggerhead stock, which were major refinements of the survival and fecundity schedules used in Richardson and Richardson (1982). The Frazer (1983, 1984, 1986) life table schedules were the first schedules produced for sea turtles and are still the only substantive static life table models available. These age-specific survival and fecundity schedules provide information useful for comparative demographic analysis. Both SPA (Marquez M et al. 1982a,b) and static life table schedules (Frazer 1983, 1984, 1986) are very useful for parameterizing age-structured simulation models discussed in the following sections.

5.1.2 Dynamic age-structured

All models assigned here (Doi et al. 1992, Crowder et al. 1994, Heppell et al. 1996) are some form of deterministic age-structured matrix model. Doi et al. (1992) used a general form of dynamic pool or so-called yield-per-recruit stock assessment model (Megrey and Wespestad 1988). The dynamic pool model used by Doi et al. (1992) is also a form of generalized Bernardelli-Lewis-Leslie (BLL) matrix (see Mohn 1986). The BLL model is a common mathematical description of density-independent growth of an age-structured population observed at discrete time intervals. The BLL matrix models used by Crowder et al. (1994) and Heppell et al. (1996) were complements of stage-structured loggerhead models so we leave these two studies until the next section.

Doi et al. (1992) developed an extended dynamic pool model to estimate optimal harvesting yield given hypothetical levels of fishing intensity for a hawksbill fishery based in Cuba. The extensions included an age-structured cohort, gradual adult maturation, a piece-wise linear age-specific harvesting risk function and a piece-wise linear Beverton-Holt type stock-recruitment function. Fishing mortality and natural mortality (hazard) were assumed to be continuous and separable functions. The model makes other major assumptions – (1) growth is well described by a von Bertalanffy function, (2) a year and cohort invariant von Bertalanffy age-length key to back transform catch-at-length to catch-at-age since age is unknown, (3) constant time invariant recruitment, (4) a constant time invariant hazard function and (5) a constant time invariant Baranov type catch function. It is a sophisticated but assumption laden model that is very common in fisheries stock assessment. It incorporated SPA (see section 5.1.1) to review transient behaviour induced by changes to model parameter inputs. Doi et al. (1992) concluded that the escapement size for hawksbills in the Cuban fishery would need to be increased to 70cm SCL (12 years old) to ensure the long-term viability of this stock.

The major concern with this model is that it was based on very little biological data about the hawksbill stock itself. Doi et al. (1992) relied on captive reared growth information (see concerns discussed in section 3.1.2 on captive studies) or theoretical inputs such as a presumed maximum exposure of immature hawksbills to the fishery no later than 7 years of age, complete sexual maturation by 14 years of age and negligible dispersal to or from the Cuban stock. There were no valid estimates of age- or size-specific natural mortality let alone a hazard function conditioned on age, year and cohort effects. Since stock abundance in foraging or nesting habitats was either unknown or poorly known the model had no empirical stock reference behaviour to assess the heuristic value of the model. Sullivan et al. (1990) present a general stochastic size-

than developmental states. Unless distributed delay maturation for each stage is incorporated (see section 5.2.1) all the deterministic stage-structured models cannot in their current form cope with time varying changes.

The BLL matrix approach was used by Crowder et al. (1995) to get around this problem. But it then introduces other problems associated with assuming all demographic responses are only age-dependent and that all responses occur only at fixed ages within a fixed 54 year life expectancy – quite a limiting set of assumptions which was the rationale for using stage-structured models in the first place. There was no empirical stock reference behaviour to assess the heuristic value of this model. Nonetheless, this is a particularly useful simulation because it provided for the first time important qualitative insights into the long time delays inherent in loggerhead population recovery following TED introduction. Crowder et al. (1995) used the Crowder et al. (1994) stage-structured model to forecast population recovery rates using revised estimates of TED-reduced mortality derived from their recent analysis of loggerhead strandings.

Laurent et al. (1992) developed a stage-structure model for a Mediterranean loggerhead stock using six stages (4 size-based stages and 2 reproductive status stages). Stage transition (maturation rate) was knife-edge and time invariant as for the Crouse et al. (1987) and Crowder et al. (1994) models. They concluded from a sensitivity analysis (elasticity) that reducing annual mortality of loggerheads larger than 70cm SCL (large juveniles and adults) was essential for stock viability. The model was based on little empirical demographic information relevant to the stock. There was no empirical stock reference behaviour to assess the heuristic value of this model.

Somers (1994) developed a stage-structured model for the sGBR loggerhead stock. This model was similar to Crouse et al. (1987), the main difference being a modified size-based classification and mainly theoretical demographic parameters reflecting the stock in a hypothetical reefal setting. Unlike Crouse et al. (1987), Somers (1994) concluded that protection of eggs/hatchlings would have a major impact on long-term stock viability. The reason for the difference in conclusion between the two studies was due to higher egg/hatchling stage mortality rates used in Somers (1994). There was no empirical stock reference behaviour to assess the heuristic value of this model.

Heppell et al. (1996) also developed a stage-structured model for the sGBR loggerhead stock. This model was similar to Crouse et al. (1987). The main difference being a stage classification for immature and adult loggerheads based on reproductive condition determined from laparoscopy. The demographic parameters were relevant to a stock in a hypothetical reefal setting and to a sGBR stock nesting at the adjacent mainland rookery (Mon Repos). This model used stage-specific survival rates for immature and mature loggerheads derived from Cormack-Jolly-Seber analysis (Lebreton et al. 1992) of capture profiles derived from a mark-recapture program (see Limpus et al. 1994b). The survivorship analysis assumed time invariant mortality confounding year and cohort effects. Stage durations were derived from the von Bertalanffy growth function presented in Frazer et al. (1994; section 3.2.3.3).

They concluded from sensitivity analysis (elasticity) that reducing annual mortality of loggerheads larger than about 70cm CCL was essential for stock viability. Like Crowder et al. (1994), Heppell et al. (1996) then used a BBL matrix form of their model with 35 age-classes to simulate time dependent responses in adult female abundance in reply to (1) levels of trawling related mortality or (2) previous fox predation of eggs at the mainland rookery. The two mortality sources were not simulated simultaneously. There were no empirical stock reference behaviours to assess the heuristic value of these models.

All the stage-structured models discussed in this section assumed time invariant and density independent demographic rates. Therefore age, year and cohort effects are

confounded. Individuals in a stage were also assumed indistinguishable with respect to growth development and time spent in that stage. In other words all individuals develop at the same rate and progress to the next stage with the same maturation rate – similar to the constant knife-edge recruitment assumption of SPA (section 5.1.1). Growth studies for many species of sea turtles (Bjorndal and Bolten 1988a, Ehrhardt and Witham 1992, Limpus 1992b, Mohanty-Hejmadi 1992, Klinger and Musick 1995, Chaloupka and Limpus 1995a) have shown significant individual variability suggesting that including variable development rates in future models might be worthwhile.

Crouse et al. (1987), Laurent et al. (1992), Crowder et al. (1994) and Heppell et al. (1996) all used sensitivity analyses based on elasticity measures. Elasticity does not recognize covariation and assumes that each trait is independent of all other traits. Yet van Buskirk and Crowder (1994) in a review of life history traits found correlation between reproductive traits. Covariation in demographic rates might well explain why several studies found stage-specific parameter insensitivity to fixed stage durations yet the most sensitive stages to the other parameters were those stages with the longest stage durations (see Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1996). Van Thenderen (1995) proposed use of integrated elasticity measures that attempt to account for correlation in traits such as survival and fecundity. Application of integrated elasticity measures might well change some of the conclusions of sea turtle studies based on deterministic linear stage-classified models.

5.2 Stochastic Simulation Models

5.2.1 Dynamical systems

Chaloupka and Limpus (1995b) developed a simulation model of the population dynamics for green turtles comprising the sGBR genetic stock. The model was a hybrid *i*-state distribution type based on a stage-classified demography comprising age-based and reproductive status-based stages and it considered both foraging and rookery areas. Age-based stage durations were derived from weibull type growth functions presented in Chaloupka and Limpus (1995a; section 3.2.3.4). The model comprised a dynamic system of stage-specific difference equations linked with demographic rates reflecting nonlinear, feedback, time varying, distributed delay and stochastic properties. It included demographic stochasticity and also environmental stochasticity due to the delayed impact of ENSO events on female breeding likelihood (see Limpus and Nicholls 1994). Mortality estimates were based on both empirical and theoretical sources. Growth and maturation were assumed to be heterogeneous processes so stage transitions were modelled as distributed-delay rates based on Erlangian functions (see Blythe et al. 1984).

The model is part of a larger heuristic modelling system designed as a tool to help understand the dynamic nature of sea turtle demography, harvesting behaviour and impact of specific conservation policies. Chaloupka and Limpus (1995b) used this simulation model to investigate the potential impact of egg harvesting on the long-term viability of the sGBR green turtle stock at all stages of the life cycle. While the temporal behaviour of most of the stages in unknown their simulation model outcomes reflected well the known annual nesting stock at Heron Island (sGBR) and long-term patterns in variability of southeast Asian green turtle nesting stocks with a known egg harvesting history (Limpus 1993). In other words this model reflected well various independent regional reference behaviours.

Sensitivity analysis was undertaken using parameter perturbation and fractional factorial sampling design (Steinhorst et al. 1978). They found that their system was sensitive to changes in the proportion of females in the foraging areas preparing to breed each year, which is itself a function of stochastic environmental factors and post-breeding return time – a finding supporting the view of Miller (1994) for the importance of conducting foraging area studies.

Chaloupka and Limpus (1996b unpublished) have designed a similar dynamical system model for the sGBR loggerhead stock to support a risk-based evaluation of trawl fishery impacts and for testing policy options to mitigate trawling risk. The model builds on the deterministic model of Heppell et al. (1996) but includes distributed delay maturation, stochastic demographic parameters and stochastic breeding likelihood. Their simulation model outcomes reflected well an empirical reference behaviour – the annual Mon Repos (sGBR) nesting stock. They used this model to assess the relative risks of trawling simultaneously with other known mortality sources on the long-term viability of this particular stock. The model complements the empirical studies on trawl related risks for sea turtles in Australian waters (see Poiner and Harris in press).

None of the models in Table 2 incorporate explicit spatial structure. The models of Chaloupka and Limpus (1995b, 1996b unpublished) can be extended to include explicit spatial structure and multispecies systems but the approach becomes awkward for modelling more than a moderate number of subpopulations or interacting species.

5.2.2 Monte Carlo process

Bustard and Tognetti (1969) designed probably the first sort of *i*-state configuration model (DeAngelis et al. 1993) to investigate sea turtle population dynamics. The model was a Monte Carlo experiment (see Rubenstein 1981) to simulate the probability of a green turtle nest being destroyed as a function of increasing female nesting density. The model was not well documented but it seems that hypothetical individual turtles were tracked over a 35 day nesting cycle as each turtle attempted to nest in a fixed beach area at 15 day intervals. The model was based on the sGBR green turtle stock nesting on Heron Island. They used the model to derive a linear function between nesting density and percentage nest destruction where every 100 additional nesters resulted in an additional 5% nest destruction – all eggs in the nest are destroyed not a portion. Bustard and Tognetti (1969) then proposed that nest destruction was a major density dependent mechanism of population regulation. Their linear numerical response function implies a dome-shaped or extreme Ricker-type stock recruitment function (see Ricker 1975). There is little basis for adopting either their linear numerical response function nor the implicit stock-recruitment function. There are no empirical records of extensive nest destruction for any nesting stock for any species in the Great Barrier Reef region. Even if such a numerical response function existed it would still be only one of many factors affecting population dynamics.

6. Conclusion

Substantial work has been carried out on growth dynamics of sea turtles, increasingly from wild stocks. Table 1 presents many of these growth studies arranged to foster easy selection of conspecific information classified by the underlying methodological approach. For instance, if information for Kemp's ridley is needed then the appropriate selection would be – (1) age cross-sectional (Zug et al. 1996), (2) age longitudinal (Marquez M 1972, Caillouet et al. 1986) and (3) age mixed headstarted (Caillouet et al. 1995). For hawksbills the selection would be – (1) age longitudinal (Witzell 1980), (2) size mixed growth interval (Limpus 1992b, Boulon 1994) and (3) size mixed nonparametric growth modelling (Chaloupka and Limpus 1996a unpublished).

Nonetheless, it is premature for a full scale comparison of sea turtle growth dynamics. Many studies relied on inappropriate growth functions, questionable tagging protocols and were fitted to limited ontogenetic ranges. Many studies fitted age- or size-based forms of the von Bertalanffy growth function yet there seems little basis for justifying this function either on empirical or statistical grounds. A necessary condition for a von Bertalanffy type function is a size- or age-specific growth rate function that is monotone decreasing over the entire post-natal development phase – this has not been shown for

any sea turtle growth study. Few studies accounted for time-dependent effects (age, year, cohort) within the constraints of the sampling design (see Table 1), which influences the validity of age estimation and growth parameter estimates. These sorts of issues will need to be considered in designing future skeletochronological and somatic growth studies for sea turtles.

Table 2 shows that many sea turtle numerical population models have been developed over the last 25 years using a variety of related mathematical approaches. All models have provided significant insight into the dynamics of sea turtle stocks and many have been concerned with conservation policy design and evaluation. We agree with Oreskes et al. (1994) that the main value of numerical models is heuristic – that is, to challenge mind sets and assumptions and encourage more focused empirical research. On this basis all the population models shown in Table 2 have been successful.

Sea turtle population modelling, however, is very much in its infancy. The limited data on size- and age-specific growth and mortality rates is a major limitation. So too is the lack of information on distribution of stage transition rates for any sea turtle stock. There are few reliable stock abundance estimates for either breeding areas or foraging areas and this was one of the reasons why many studies failed to provide an empirical stock reference behaviour to assess the model's heuristic value. Little is also known of the functional responses of sea turtle stocks to food availability in the foraging areas and whether there are any time-dependent or density dependent effects. Less is known about post-recruitment dispersal rates and spatial population structure. Even less is known about the pelagic developmental habitat and post-pelagic recruitment rates.

Estimating demographic rates and the inherent variability in those rates represents a major challenge for sea turtle research programs. Long-term mark-recapture programs coupled with reliable tagging and innovative techniques such as skeletochronology, biotelemetry and laparoscopy should form the foundation of such a research program. Clearly many such programs are well in place and we can expect to start reaping the benefits over the next few years.

7. References

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