

Hawaiian green sea turtle population model forum

11-12 February, 2002

Washington Room, Imin Conference Centre
East-West Centre, University of Hawaii-Manoa

Overnight accommodation (10-11th February) has been arranged at
Lincoln Hall, University of Hawaii-Manoa, which is next to the East-West Centre

Workshop purpose

The US National Marine Fisheries Service (Honolulu Laboratory) have commissioned Dr Milani Chaloupka (CRC Coastal, Australia) to develop interactive simulation models of the population dynamics of several sea turtle species that are exposed to competing mortality risks. The at-risk stocks are the Pacific leatherback, loggerhead and Hawaii green sea turtle stocks exposed to various human-related hazards in Pacific waters. A preliminary spatially explicit model has been constructed that incorporates all available information on green sea turtle ecology that is relevant to modelling long-term viability of the Hawaii green sea turtle stock.

The purposes of the workshop are to —

- introduce a forum of green sea turtle experts and managers to the model
- explain and demonstrate the interactive stochastic modelling approach being adopted
- enable the forum to review inputs and model assumptions incorporated in the model
- enable the forum to interact with the model in a structured way to collectively explore model assumptions, data inputs and to review expected population responses to risk factors effecting the long-term viability of the Hawaiian green sea turtle stock

Schedule

Monday February 11, 2002

0900 Welcome — Dr Michael Laurs (Director, NMFS Honolulu Laboratory)

0915 Introduction to workshop approach — Dr Milani Chaloupka

0930 Summary of model structure — Dr Milani Chaloupka

1000 Interactive model review — all participants

- stock identification
- somatic growth behaviour
- age, size, sex and spatial structure

- 1030 Break
- 1045 Interactive model review — all participants
- fecundity
 - female breeding probability
 - ageclass-specific survival probabilities
 - ageclass-specific dispersal behaviour
 - compensatory effects (breeding probability, ageclass-specific survival)
- 1230 Lunch (provided)
- 1315 Interactive model review — all participants
- compensatory effects (probability of finding mates)
 - population trends
 - environmental and demographic stochasticity
- 1445 Break
- 1500 Interactive model review — all participants
- other demographic factors not yet considered
 - identification of competing mortality risks
 - identification of population viability scenarios
- 1600 Model application — Dr Milani Chaloupka
- model sensitivity analysis approach (fractional factorial sampling)
 - demonstration scenario runs
- 1700 Day 1 conclusion
- DINNER (downtown Honolulu)

Tuesday February 12, 2002

- 0900 Play with model — all participants
- scenario runs and test assumptions
 - use model switches to turn on and off environmental effects
- 1030 Break
- 1045 Summary of workshop — Dr Milani Chaloupka
- 1115 Workshop close — Dr Michael Laurs
- 1130 Day 2 conclusion

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WORKBOOK

Hawaiian green sea turtle simulation model development

February 2002, Honolulu

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1.0 Stock definition

The green sea turtles resident in Hawaiian waters comprise mainly one distinct stock (Bowen et al 1992, Dutton et al 1997) although green turtles from the east Pacific stock are recorded occasionally in Hawaiian waters. The Hawaiian green turtle stock is increasing in abundance following severe depletion due to various anthropogenic hazards (Fig 1). Other Pacific green turtle stocks are stable such as the stock resident in sGBR waters (Chaloupka & Limpus 2001) while others such as the east Pacific genetic stock are apparently in serious decline. The at-risk stock being addressed here is the Hawaiian genetic stock that nests on the coral cays of the northwest Hawaiian Island chain. This stock apparently resides only in Hawaiian waters and is caught incidentally in Hawaii-based pelagic longline fisheries (Dutton et al 1997). The stochastic simulation model developed here is designed to explore the metapopulation dynamics of the Hawaiian stock and the risk to stock viability given exposure to various anthropogenic hazards over the last 50 years.

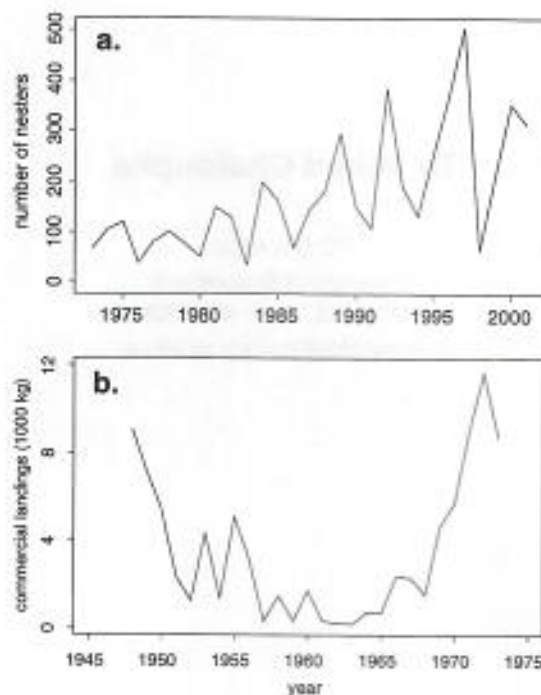


Figure 1 Time series plot of (a) estimated number of female green sea turtles nesting each year at the French Frigate Shoals rookery (1973-2001) and (b) commercial landings of green turtles from 1947-1973. Source: (a) Balazs & Wetherall (2001), (b) Balazs (1980).

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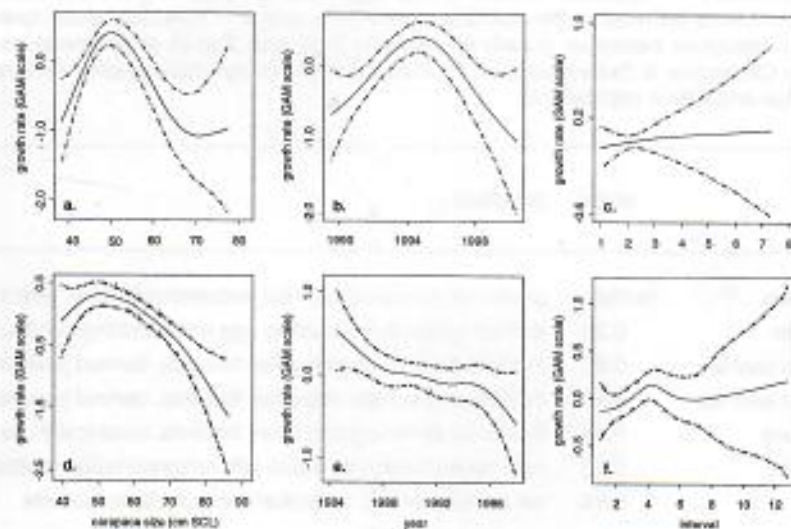


Figure 2 Somatic growth behaviour for the (a-c) Kaneohe Bay and (d-f) Molokai populations. Panels (a,d) show GAM model smooths of size-specific growth rate functions (solid curve) with a distinct growth spurt around 50-55 cm SCL. Panels (b,e) shows GAM model smooth of year-specific growth rate functions with decreases in immature growth rates during the early 1980s and late 1990s. Panels (c,f) show the GAM model smooth of sampling interval specific growth rate functions that indicates that growth rates were not a function of sampling interval durations. Dashed curves show 95% point-wise confidence curves.

2.0 Somatic growth behaviour

Hawaiian greens recruit from the pelagic habitat to the benthic habitat in coast waters in the Hawaiian Archipelago at ca 35 cm SCL (Balazs 1980). The pelagic phase duration for Hawaiian greens is estimated to be at least 5-7 yr (Zug & Balazs 2000, Zug et al in press).

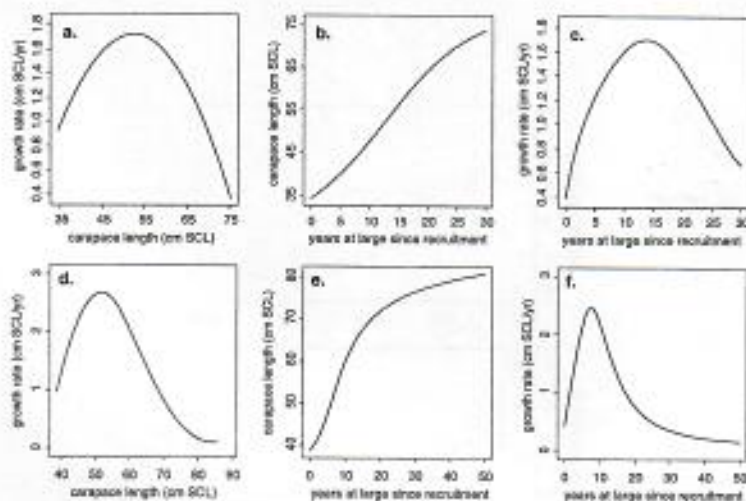


Figure 3 Estimated age- and size-specific growth functions for green turtles resident in foraging grounds in (a-c) Kiholo Bay (Hawaii) and (d-f) Punalu'u (Hawaii). Kiholo functions derived from a GAM model while Punalu'u functions derived from a local regression model. Panels (a,d) reproduce the size-specific growth function that were integrated numerically to give the expected size-at-age (age ~ years-at-large since recruitment) function shown in (b,c), which were differentiated numerically to give the expected age-specific growth rate functions (c,f).

Table 1 Summary of ageclass structure and ageclass-specific survival estimates and sampling probability density functions included in the stochastic simulation model of Hawaiian green turtle metapopulation dynamics. Ageclass structure based on growth functions in Fig3 and Zug et al (in press); survival probability functions based on Chaloupka & Balazs (unpubl) for CJS analyses of ageclass-specific survival probabilities for the Kaneohe, Molokai and Kiholo populations.

ageclass	stage	mode	comment
0	hatchling	multiple	predation, poaching/harvest, erosion/wash-over, beach temperature
1	neonate	0.25	derived parameter including egg and hatchling survival, <i>ev</i> pdf
2-7	pelagic juvenile	0.60	incidental drowning and other hazards, derived parameter, logistic pdf
5-15	benthic juvenile	0.80	incidental drowning and other hazards, derived parameter, logistic pdf
15-25	immature	0.85	incidental drowning and other hazards, empirical basis, logistic pdf
25-40	subadult	0.90	right skewed extreme value pdf, empirical basis, multiple hazards
40+	adult	0.95	left skewed <i>ev</i> pdf, empirical basis, multiple hazards

Size-at-age data for Hawaiian greens was analysed by Zug & Balazs (2000) and Zug et al (in press) using skeletochronological procedures. Recently, Chaloupka & Balazs (unpubl) analysed large data sets for several foraging ground populations of the stock (Figs 2-4) using a 2-stage nonparametric modelling procedure (Chaloupka & Limpus 1997, Limpus & Chaloupka 1997, Bjorndal et al 2000, Chaloupka 2001b). It is also apparent that somatic growth of immature Hawaiian greens has declined over the last 10 years or so (Fig 4), which is consistent with a density-dependent effect on somatic growth and presumably age at sexual maturity as the stock recovers (Fig 1a). Sex-specific growth is well known for other green sea turtle stocks (Limpus & Chaloupka 1997, Chaloupka 2001b) but no sex-specific data are available for the Hawaiian stock so it is assumed in the model that males and females display similar growth.

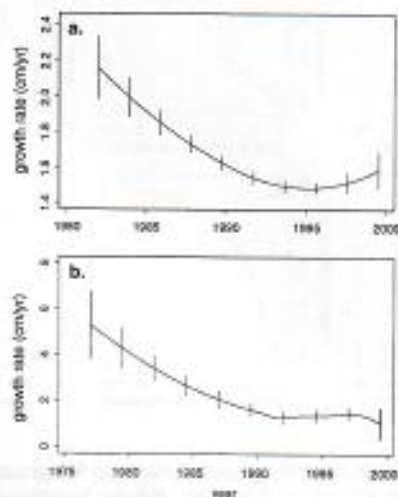


Figure 4 Time-dependent growth rates for immature greens resident in (a) Kiholo Bay and (b) Punalu'u derived from local regression models with 95% pointwise confidence intervals shown at 10 equally spaced intervals. See Loader (2000) for a detailed discussion of local regression models.

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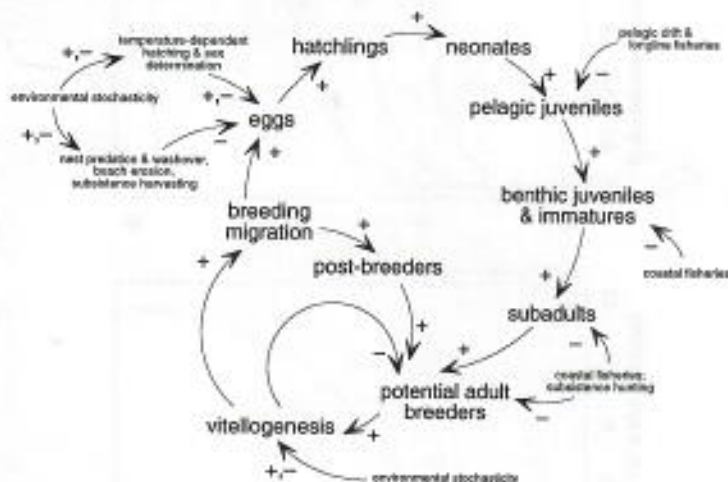


Figure 5 Developmental phase- and reproductive-status based lifecycle graph or causal loop model (Puccia & Levins 1985) for Hawaiian green turtles. This is the demographic structure and feedback mechanisms included in the stochastic simulation model to explore Hawaiian green turtle metapopulation dynamics subject to various hazards (eg., nesting beach erosion, nest inundation by wave washover, egg and turtle harvesting, or incidental capture and drowning in coastal or pelagic fisheries).

3.0 Age-size-sex-spatial structure

Given the age-specific findings in Zug et al (in press) and the size- and age-specific findings in Figs 2-3, it is apparent that Hawaiian greens are ca 25-40 yr old at maturity, which is consistent with estimates for the sGBR green sea turtle metapopulation (Chaloupka et al in press). The derived ageclass structure for the simulation model given these considerations is summarised in Table 1, which includes the distributed recruit from 5-7 years from the pelagic phase to the benthic juvenile phase. The model comprises 2-subpopulations reflecting the southeastern Hawaiian Islands substock and the northwestern Hawaiian Islands substock — the final model is proposed to comprise 4 substocks (Northwest, Kauai/Oahu, Molokai/Maui, Hawaii). The substock structure is based on the observations that (1) there is strong foraging ground fidelity and (2) little immature dispersal between foraging grounds (Balazs 1980, Balazs et al 2000). Once recruited to a benthic foraging ground, there is then little evidence for either ageclass- or sex-specific dispersal behaviour (Balazs 1980, Balazs et al 2000). The pelagic juveniles recruit as benthic juveniles from ca 4-7 yrs. The recruitment function for pelagic juveniles recruiting to the coastal benthic habitat is assumed to be the following age-specific function (probabilities are changeable in the model using interactive slider devices —

- probability of a 4 yr old pelagic juvenile recruiting as a 5 yr old benthic juvenile = 0.05
- probability of a 5 yr old pelagic juvenile recruiting as a 6 yr old benthic juvenile = 0.25
- probability of a 6 yr old pelagic juvenile recruiting as a 7 yr old benthic juvenile = 0.50
- probability of a 7 yr old pelagic juvenile recruiting as a 8 yr old benthic juvenile = 1.00

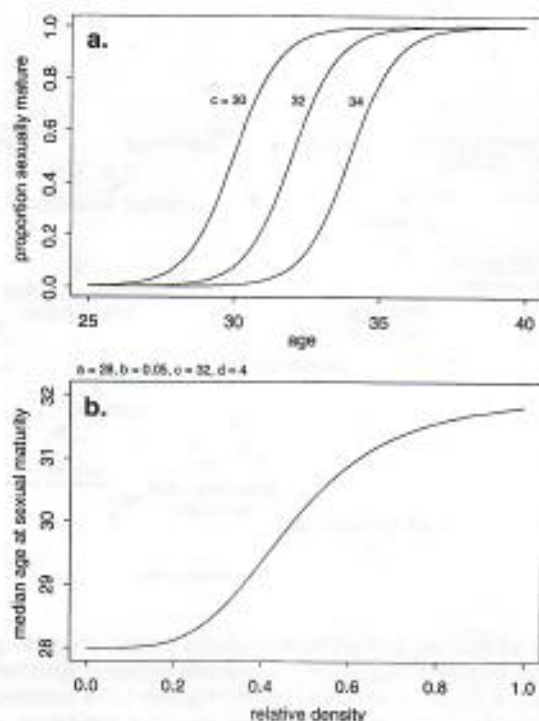


Figure 6 Panel (a) shows various forms of the logistic age-specific maturity function [$y = 1/(1+\exp(-a*(age-b)))^c$], which is adjustable by using an interactive slider device. Here the 'b' parameter is varied to show some of the age-specific maturity functions that can be applied in the model to evaluate model sensitivity. The 'b' parameter = median age at maturity when the 'c' parameter = 1, if 'c' < 1 then 'b' > median while if 'c' > 1 then 'b' < median age at maturity. Panel (b) shows the 'c' parameter as a Morgan-Mercer-Flodin function of relative benthic substock density used here to invoke density-dependence in the age-at-maturity function shown in (a).

The immature duration is estimated ca 10 yrs (15-25 yrs old, Table 1). The subadult or maturing adult duration is estimated ca 15 yrs (25-40 yrs old, Table 1) with the assumed age-specific maturation functions shown in Fig 5b, which were derived from size-specific maturation data for male and female loggerheads (Fig 6a), which is assumed to be density-dependent (Fig 9b) given the apparent somatic growth declines shown in Fig 4. A common age-specific maturity function is the default in the model although sex-specific maturity is accommodated by parameter adjustments to the maturity functions using interactive sliders devices. Adults are 40+ years old with 100% sexual maturity assumed. The ageclass/stage structure in the model is summarised in Fig 5 (Table 1), which includes the major sources of mortality risk and the key environmentally influenced demographic processes. The major environmental effects in the model are concerned with breeding behaviour (Fig 9a) and temperature dependent hatching probability (Fig 8a). Hatchling sex ratio is also temperature dependent (Fig 8b) and implemented in the model given a stochastic beach temperature generator based on nest temperature assuming a 1:1 sex ratio (Wibbels et al 1993). While the model is sex structured, its default setting is for sex-specific differences in breeding probability functions but no sex-specific differences in maturation or survival probability functions. However, all settings are readily changed in the model using interactive slider devices.

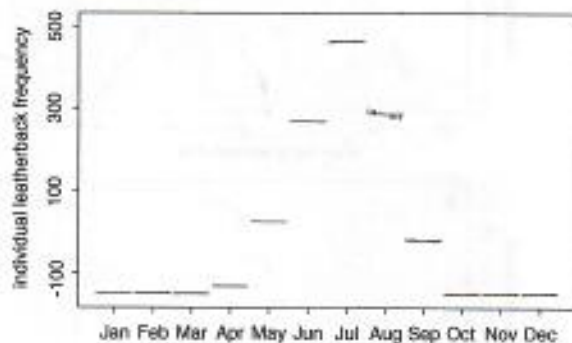
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Figure 7 Seasonal cycle monthly subseries plot of number of female leatherbacks recorded on beach at Rantau Abang, Terengganu, Malaysia (1967-1976). The plot shows the fitted seasonal component from an STL analysis (see Chaloupka 2001a) that provides an assessment of the historical seasonal pattern as well as the temporal behaviour of each monthly subseries over the 10 yr data series. The horizontal line is the fitted mid-mean value of the seasonal component for each month. The fitted values for each year (ends of the vertical lines) associated with each midmean show the pattern of interannual variation of the monthly subseries.

4.0 Fecundity

The simulation model is based on an annual cycle with no internal seasonal structure — the model simulates annual sex- and ageclass-specific abundance for the Hawaiian green sea turtle metapopulations. Many sea turtle populations nest year-round but there is usually a seasonal cycle (Fig 7), so modelling annual rather than monthly abundance is justified for the purposes of this model. The seasonal nesting cycle is apparent for the Hawaiian greens (Balazs 1980), further justifying use of an annual rather than a monthly period model. Mean clutch size or eggs per clutch (mean EPC = 104) was sourced from Balazs (1980) and is consistent with estimates for other green turtle stocks (Mortimer & Carr 1987, Bjorndal & Carr 1989). This was sampled in the model as a Poisson random variate with $\mu = 104$, which provides a pmf that is consistent with the summary in Balazs (1980). There is some evidence for seasonal variation in clutch size at other rookeries but the effect is limited (Mortimer & Carr 1987, Bjorndal & Carr 1989) and no such effect is apparent at the FFS rookery (Balazs 1980). There is some evidence for increasing clutch size with age at the rookery (Balazs 1980) but any effect would have limited demographic impact when discounted for survivorship of ageing females. Mean number of clutches laid per season (mean CPS = 1.8, max = 6) was sourced from Balazs (1980) and is lower than estimates for other green stocks (Limpus & Reed 1985, Johnson & Ehrhart 1996). This parameter was sampled in the model as a binomial random variate [$\text{bin}[p = 0.29, n = 6]$], which provides a pmf consistent with the summary information presented in Balazs (1980).

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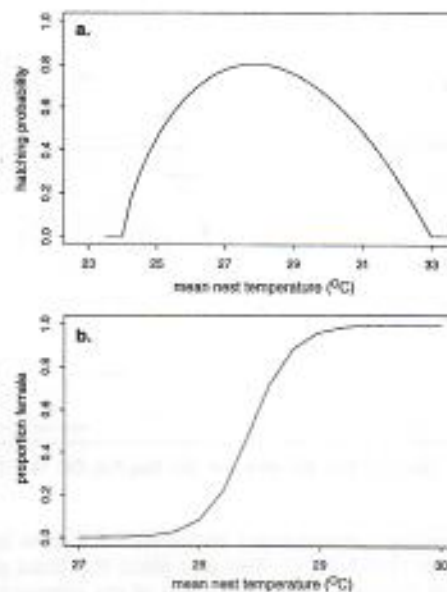


Figure 8 Functional form assumed for (a) temperature-dependent Hawaiian green turtle hatching probability and (b) temperature dependent hatchling sex determination. Curve in (a) is based on a Thornley-type model for hatching probabilities known for other sea turtle species. Curve in (b) shows a generalised logistic function for hatchling sex determination probabilities known for other sea turtle species. All functional forms in model are readily adjustable by using interactive slider devices.

5.0 Temperature-dependent hatching probability and sex determination

Green turtle hatching success rate or probability is assumed to be a direct function of nesting temperature during the incubation as it is for other sea turtle species (Limpus & Reed 1985, Godfrey et al 1996, Binckley et al 1998). There are no readily available data for deriving the temperature-dependent functions for the Hawaiian stock so data for other species was used. The functional form assumed here (Fig 8a) was derived from a Thornley-type nonlinear model fitted to data for sea turtle species (Limpus & Reed 1985). The simulation model then uses a stochastic beach temperature generator to derive annual nest temperature that is consistent with mean seasonal nest temperature for the FFS rookery and an equal primary sex ratio (Wibbels et al 1993) — but see Balazs (1980). The simulated nest temperature for that season then forms the basis for expected hatching probability for that simulation year. Limpus & Reed (1985) and Binckley et al (1998) provided experimental data for other sea turtle species that was used here to derive the temperature-dependent hatchling sex ratio process for the green turtle model. The functional form that best fits these data was a generalised logistic function (Fig 8b). The 2 forms shown in Fig 8 are generic for the Hawaiian green turtle metapopulation and need to be verified with experimental data — all functional forms in model are readily adjustable by using interactive slider devices.

Comments:

6.0 Expected breeding behaviour

Balazs (unpubl 2002) provided a data set comprising 1847 records of the remigration interval for female greens nesting on East Island, French Frigate Shoals rookery (see Fig 9a). These data were used to derive the expected probability of female breeding each year, which was based on fitting various probability density functions to the reciprocal of the data in Fig 9a. The best fit probability density function (pdf) to the derived annual proportion of females breeding was an extreme value pdf (Fig 9b, solid curve). The expected male breeding probability function (Fig 9b, dashed curve) was derived by offsetting the estimated female pdf given the assumptions in Balazs (1980) that Hawaiian males have a shorter remigration interval than females — a view that is consistent with males from other green turtle stocks (Limpus 1993, Limpus et al 1994). The fluctuations in breeding behaviour (environmental stochasticity) are assumed implicitly in the model to be a function of fluctuating food supply effecting accumulation of body fat needed for vitellogenesis and migration (Kwan 1994).

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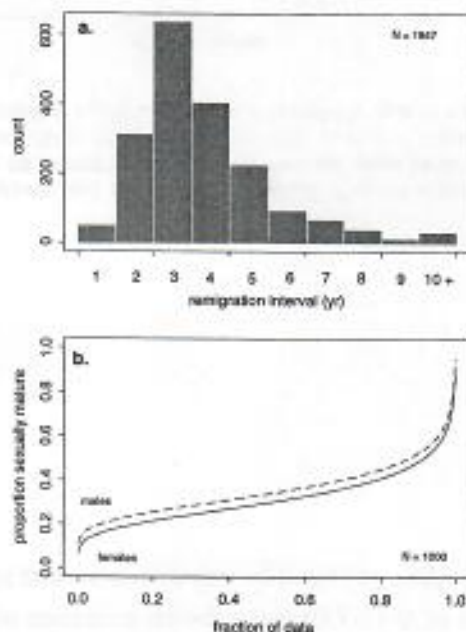


Figure 9 Panel (a) shows estimated remigration interval (years) for females nesting on East Island (French Frigate Shoals) from 1973-2001. Panel (b) is a quantile plot based on a right skewed extreme value pdf showing the derived proportion of females preparing to breed each year (solid curve) - based on Balazs (1980). It is assumed that males have a higher probability of preparing to breed function (dashed curve).

7.0 Ageclass-specific survival probabilities

There are few reliable ageclass-specific estimates of green sea turtle survival probabilities (see review in Chaloupka & Limpus 2001b). The following estimates were derived from various sources (Gyuris 1994, Chaloupka & Limpus 1998, Chaloupka & Limpus 2001b, Chaloupka 2002) and extensive CJS modelling of ageclass-specific survival probabilities for

several foraging populations of the Hawaiian stock for the purposes of model development (Table 2, Fig 10). Most of these estimates and assumed pdfs are also consistent with robust estimates derived using long-term mark-recapture studies for green turtles resident in sGBR waters (see Chaloupka & Limpus 2001a,b). Some ageclass-specific estimates were derived using model tuning (Table 1). There are no apparent sex-specific difference in green sea turtle survival (Chaloupka & Limpus 1998, Chaloupka 2002) although the model includes sex-specific survival probability functions should such information become available.

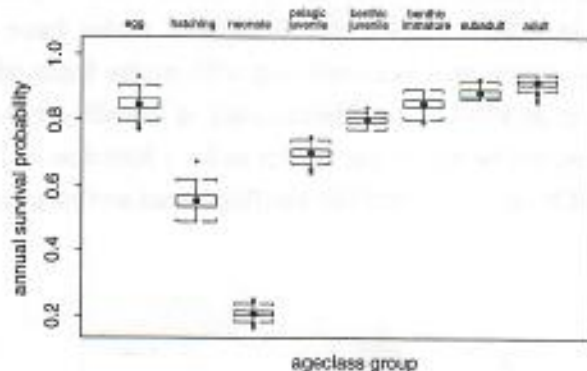


Figure 10 Boxplot summaries of the ageclass- and stage-specific annual survival probabilities from 1000 model runs of the stochastic simulation model of Hawaiian green turtle metpopulation dynamics (see also Table 1). Pelagic juvenile survival probabilities were derived here by model tuning as there are no empirical estimates for this ageclass. All ageclass-specific survival probability functions are readily adjustable in the model using interactive slider devices.

Comments:

8.0 Compensatory effects

The expected sex-specific breeding probability was also assumed in the model to be a density-dependent function. Bjorndal et al (2000) have shown evidence of density-dependent effects on green turtle growth that were assumed to be related to declining per capita food availability as the population increased. It is reasonable to assume that food availability might also have an effect on loggerhead breeding behaviour. Moreover, many marine vertebrate populations do recover from significant levels of harvesting but this recovery can take a long time for sea turtles so that any density-dependent effects in the model need to be readily amended in light of new information. Hence, the model includes a switch to turn on or off any density-dependent functions to evaluate the effect of including density-dependence and the assumed functional form of that dependence on model performance and sensitivity. The assumed sex-specific functional forms are shown in Fig 11, which was based on a Morgan-Mercer-Flodin function where $y = (a \cdot b + c \cdot X^d) / (b + X^d)$ and $(a-d)$ are estimable or adjustable parameters, $y =$

expected proportion preparing to breed each year and $X = (1 - \text{relative density})$. The Morgan-Mercer-Flodin function is flexible with good statistical fitting properties (Ratkowsky 1990) and is adjusted in the model to correct for new information or to evaluate the effect of different functional forms on model performance and sensitivity. Special cases of the Morgan-Mercer-Flodin function include the rectangular hyperbola, the Michaelis-Menten-Monod, the Holling Types I-III and the Hill functions that are used to reflect growth, nutrient uptake, predator consumption or density-dependent demographic functions.

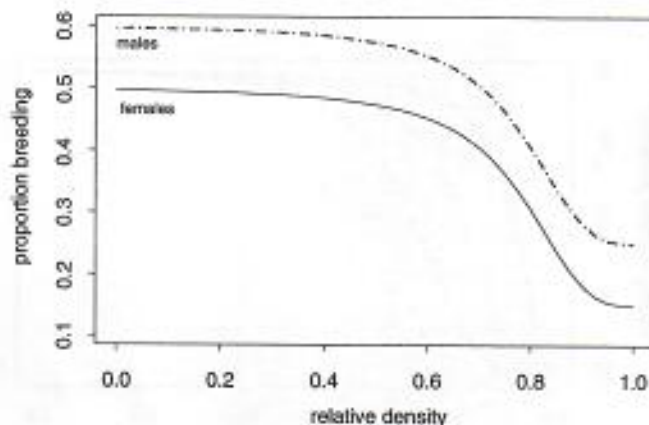


Figure 11 Density-dependent sex-specific probability of breeding functions for Hawaiian greens. Solid curve shows female annual breeding probability function as a function of the relative benthic substock density. Dashed curve = male breeding probability function. The assumed functional forms are easily changed in the model using interactive parameter slider devices. The functional form used here is based on the Morgan-Mercer-Flodin function that includes other common functional forms as special cases.

Comments:

9. Depensatory effects

The actual number of females breeding and then nesting depends not only on preparing to breed and migrating to the regional rookery but also the probability of actually finding at least 1 male to mate with in the courtship grounds. For instance, if many females are ready to mate but there are too few males then many potential pregnancies will not be realised due to the male shortage. This is a form of depensatory density-dependence known as an Allee effect (Dennis 1989) that is an important process affecting the recovery or rebound capacity of populations exposed to perturbations such as harvesting or a run of ecological catastrophes. The mating success probability function used in the model was based on a Morgan-Mercer-Flodin function (Fig 12), where: $y = (a \cdot b + c \cdot X^d) / (b + X^d)$, ($a-d$) are adjustable parameters, y = probability of a female in the courtship grounds finding and mating with at least 1 male and

X = relative density of mature males assuming they migrated to the courtship grounds. This form based on relative density is adopted here mainly to implement sex-biased harvesting or loss potential in the model and assumes that it is the relative abundance of females to males that effects the probability of encountering a mate in the courtship grounds. It is also assumed here that there is some form of competition between females for mates. It is important to note that the functional form in the model shown in Fig 12 is generic and not based on empirical data for the Hawaiian green stock. Nonetheless, the function is readily adjusted to reflect other forms if necessary and to evaluate the effect of various forms on model performance and sensitivity.

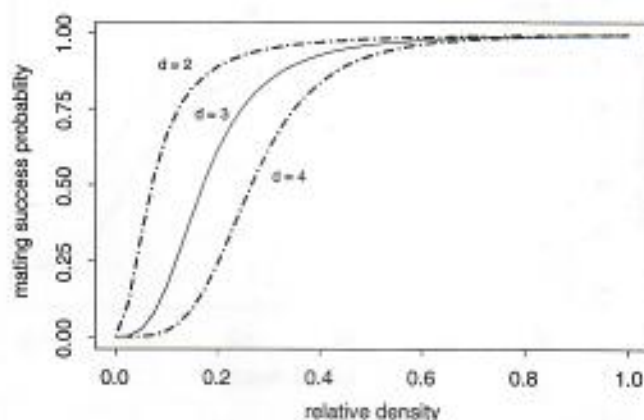


Figure 12 Density-dependent female mating success function (probability of an Hawaiian female green turtle finding and mating with at least 1 male given relative density of breeding males and females in the courtship grounds. Solid curve shows function setting in model while the 2 dashed curves show other forms possible in model by simple changes to a specific parameter setting.

Comments:

Table 2 Summary of metapopulation abundance estimates for the Hawaiian green sea turtle stock based on Horwitz-Thompson type abundance estimates (Chaloupka & Balazs (unpubl). See Chaloupka (2000) and Chaloupka & Limpus (2001a) for details of Horwitz-Thompson type estimation of sea turtle abundance.

population	ageclass	abundance		comment
		mean	(95% CI)	
Kaneohe	juveniles-immatures	456	225-668	steady ca 450
Molokai	juveniles-immatures	2226	590-3578	steady at ca 2500
Kiholo	juveniles-immatures	178	122-234	steady ca 250 possibly declining

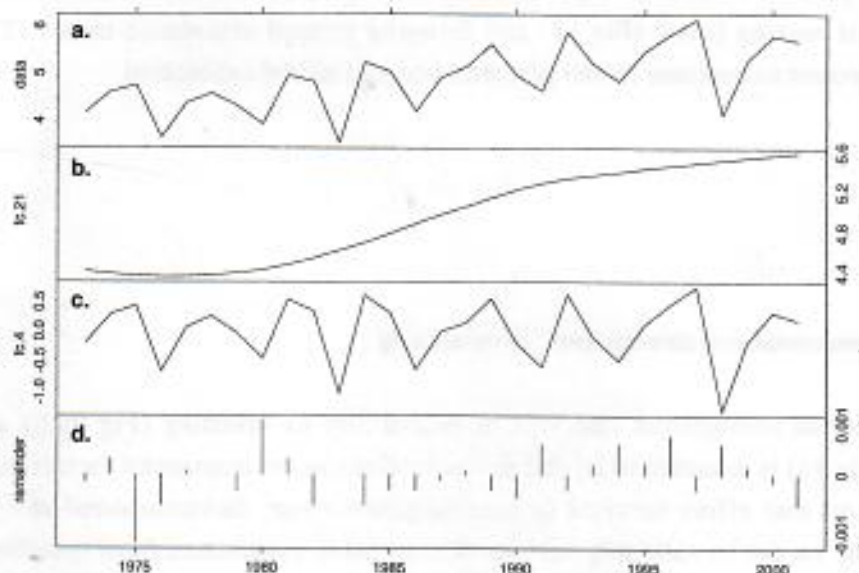


Figure 13 STL decomposition plot of the estimated number of female green turtles nesting each at the French Frigate Shoals rookery (1973-2001) — note the log scale. Panel (a) estimated annual nesting series. Panel (b) fitted long-term trend or low-frequency variation in estimated number of nesters (bandwidth of trend filter = 21 yr). The maximum rate of increase in the long-term trend occurred ca 1986-1987. Panel (c) fitted 3-4 year quasi-periodic trend or high-frequency variation in estimated nesters (bandwidth of trend filter = 4 yr). Panel (d) residual component remaining after the trend (panel b) and quasi-periodicity (panel c) components have been fitted to the series. The 3 components shown in panels (b to d) sum exactly to the series shown in panel (a). The panel scales are not the same so the vertical bar at the right of each panel indicates relative variation in scaling amongst the components and original data series. Hence the trend and quasi-periodicity are substantial components of the original realisation shown in panel (a). The residual component (panel d) is negligible as the frequency components in panels (b,c) account for >99.9% of the data series in panel (a). See Chaloupka & Osmond (1999) and Chaloupka (2001) for details of time series decomposition methods based on robust nonparametric regression modelling such as STL, which uses loess smoothing methods (Cleveland et al 1990).

10. Population trends

Population trends can be a useful measure of stock status and condition when used cautiously (Bjorndal et al 1999, Chaloupka & Limpus 2001a). Trends also provide one basis for simulation model evaluation by serving as an empirical benchmark to assessment model performance. Chaloupka & Balazs (unpubl) estimated the ageclass-specific abundance of Hawaiian green turtles in several foraging ground populations of the stock (Table 2). These estimates were derived using a Horwitz-Thompson type estimator based on CJS estimates of ageclass-specific recapture probabilities (see Chaloupka 2000, Chaloupka & Limpus 2001a). These estimates provide a basis for deriving density estimates and an estimate of the overall metapopulation abundance — useful for initialising the simulation model. Balazs & Wetherall (2001) provide an estimate of the number of females nesting each season at East Island in the French Frigate Shoals rookery (Fig 1a, Fig 13a), which accounts for ca 55% of the Hawaiian nesting population (Balazs 1980). A time series decomposition analysis of these data is shown in Fig 13 using a robust nonparametric procedure (Chaloupka 2001a). The most important feature of these data is (1) the increase but at a slowing rate for the nester series (Fig 13b), which is consistent with density-dependent processes in affect as the stock increases and (2)

the quasi 3-4 year periodicity in nester abundance (Fig 13c), which is also consistent with Fig 9a. The use of nesting beach (Fig 13) and foraging ground abundance trends (Table 2) are used in this project to evaluate model performance and model calibration.

Comments:

11. Environmental and demographic stochasticity

The variability in remigration intervals or probability of breeding (Fig 9a,b) and nesting variability (Fig 1a) is assumed to be due to fluctuations in environmental factors such as SST, food and so on that effect survival or breeding behaviour. Environmental stochasticity is included in the model by sampling various demographic parameters from specified pdfs that reflect both measurement error and environmental stochasticity. The model does not explicitly account for what are the factors driving the environmental stochasticity, except for beach temperature. Chaloupka (2001a) has shown that regionally synchronised nesting fluctuations for southeast Asian green sea turtle populations (hence interannual variability in breeding probability) was most likely due to fluctuations in SST and hence ENSO events. This may also be correct for Hawaiian greens (Fig 1a) but there is no empirical basis for this view so no attempt has been made here to explicitly link breeding behaviour to ENSO events, although this has been done elsewhere (Chaloupka 2002). The model also includes demographic stochasticity (see Engen et al 1998). For instance, the expected number of clutches was also subject to demographic stochasticity by using a binomial sampling approach (Akçakaya 1991) with expected clutch size and expected number of nesting females. The actual number of hatchlings was subject to demographic stochasticity by sampling expected number of clutches, clutch frequency and egg survival probabilities using Poisson sampling (Brillinger 1986, Gustafsson 2000). The hatchling sex ratio in the simulation model is subject to demographic stochasticity using binomial sampling (Akçakaya 1991), as suggested by Brook et al (2000).

Comments:

12. Other demographic factors not yet considered

Other demographic processes that are not apparent in the model but could be important are canvassed here ...

Comments:

13. Other competing risk not yet considered

It was important to model simultaneously all anthropogenic hazards because of the problem of competing risks (Chiang 1991). The point is that a turtle cannot be killed twice and so mortality risks are not additive making it difficult to quantify cause-specific effects in the presence of competing risks. The model includes the capacity to account for cause-specific mortality using a multiplicative competing risks approach (see Chiang 1991). Three forms of harvest strategy or loss functions that might be attributable to incidental drowning in pelagic or coastal fisheries or minor losses due to boat strikes are explicitly accounted for in the model —

- constant rate or loss (Getz & Haight 1989)
- constant offtake or loss (Getz & Haight 1989)
- threshold-based including pure and proportional forms of harvesting of subadult and/or adult loggerhead turtles with or without stock assessment uncertainty (Lande et al 1997)

Other hazards to long-term Hawaiian green stock viability are canvassed here for model inclusion and include (Fig 1b; Balazs 1980, Kwan 1991, Wetherall et al 1993, Horikoshi et al 1994, Witzell 1994, Robins 1995, Poiner & Harris 1996, Dutton et al 1997, Slater et al 1998, McCracken 2000) —

- coastal hazards from setnet or poundnet fisheries (?-?)
- non US based longline fisheries (1985-?)
- Hawaii-based longline fishery (1985-2000+)
- pelagic driftnet fishery (1977-1991)
- subsistence harvesting around the Hawaiian islands
- egg harvest and nesting habitat loss

Comments:

14. Identification of plausible model scenarios

Comments:

16. Model sensitivity analysis approach

Model validation is concerned with evaluating whether the simulation model is acceptable for its intended use given various performance criteria (Rykiel 1996) and is assessed here using 2 approaches — (1) assessment of model capability to produce outputs that mimic qualitatively a range of empirical information including stock reference behaviours such as population trends or time series characteristics such as reddened spectra of annual nesting abundance (see Chaloupka 2001a) and (2) multi-factor sensitivity analysis based on fractional factorial sampling (Cochran & Cox 1957, Steinhorst et al 1978, Henderson-Sellers & Henderson-Sellers 1996,) within a Monte Carlo framework (Fishman 1996) — (see Chaloupka 2002 for a sea turtle example). This approach is used to identify the demographic parameters that affect model behaviour the most and to determine if those parameters were then estimated with sufficient accuracy. An example derived from a recently developed model of Western Pacific leatherback metapopulation dynamics is shown in Fig 14 for illustrative purposes.

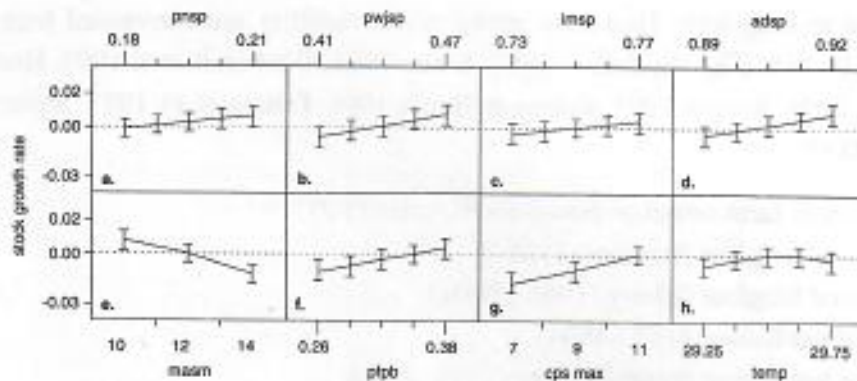


Figure 14 Parameter sensitivity analysis. Prediction profile plot showing the effects of simultaneously changing 11 major demographic parameters on predicted '15 year moving average' stock growth rate smooth in accordance with a $FF3^{11}$ sampling design. The 8 significant parameter-specific prediction traces shown above by solid curves and the 95% confidence intervals shown by error bars were derived from a weighted-variance ANOVA model. Dashed line shows a specific combination of parameter levels that was predicted to yield a zero growth rate.

Comments:

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Hawaiian green sea turtle simulation model

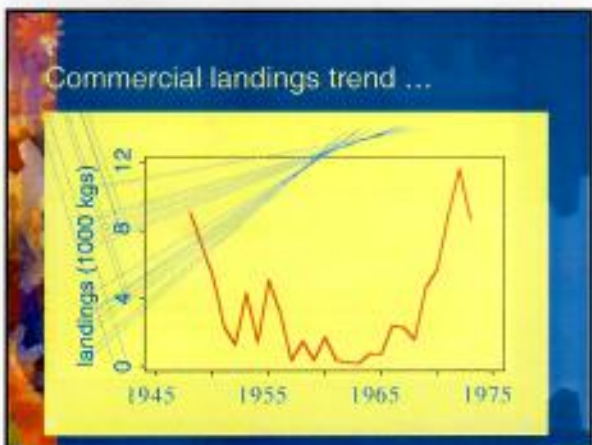
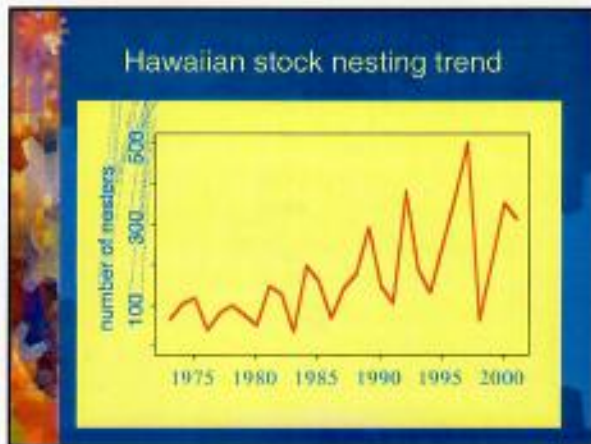
Dr Milani Chaloupka
NMFS Project #02ABW101142



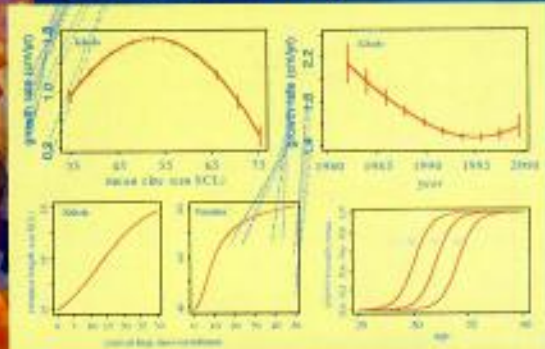
CRC for Coastal Zone, Estuary & Marine Management

Purpose

- account for Hawaiian green sea turtle metapopulation demography
- explain heuristic modelling
- demonstrate simulation model
- explore assumptions and functions
- explore competing risk factors affecting population viability
- basis for further model development



Growth and maturity ...



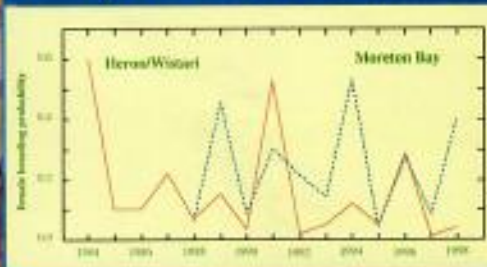
Key demographic processes



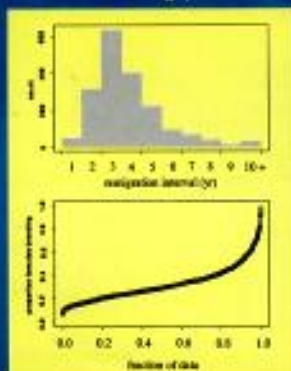
Birth (reproduction)

- year-to-year and sex-specific variability in breeding probabilities
- density-dependent and correlated
- seasonal nesting but little seasonal variability
- fecundity and sex-ratio include demographic stochasticity
- temperature-dependent hatching probabilities and hatching sex-determination

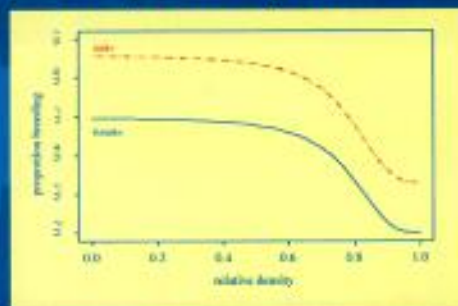
foraging ground-specific breeding probabilities (CJ Limpus)



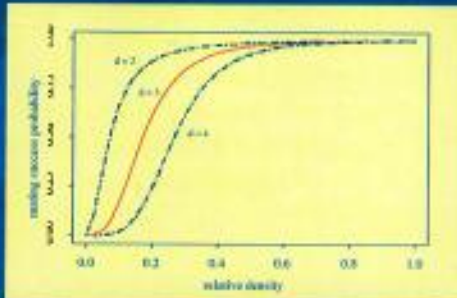
extreme value breeding probability functions



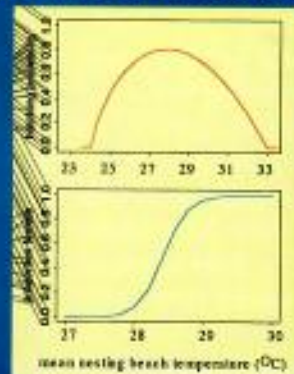
Compensatory effects



Depensatory effects



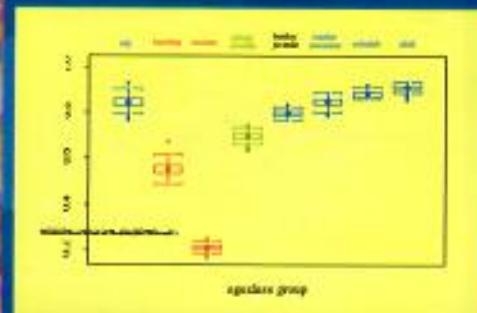
temperature dependent functions



Survival (mortality)

- ageclass-specific
- adult ageclass is high (>92%)
- negligible environmental variability
- no sex- but habitat-specific differences
- survival probabilities are correlated with between sexes and between some ageclasses
- competing risks model

Survival probabilities (sGBR greens)



Dispersal

- apparent foraging ground fidelity
- perhaps limited immature dispersal that might be distance dependent
- no apparent sex-biased dispersal
- is spatial structure important?

Heuristic simulation model

- heuristic meanings insight and learning
- model is sex- and ageclass-structured
- model is stochastic (environmental and demographic)
- demographic processes are density-dependent and correlated
- model also accounts for metapopulation or spatial structure (2 or 4 habitat?)

- model is fast and interactive to function as a learning tool
- model also useful for risk assessment and conservation policy design
- model based on extensive empirical information (GH Balazs)
- model subject to extensive evaluation to help ensure fit for use

- ### Model evaluation
- stock reference behaviours (eg., nesting abundance trends)
 - parameter sensitivity analysis based on robust experimental design procedures
 - important to determine model limitations and validity

