

Investigation on Risk-Targeted Seismic Design Criteria for a High-rise Building in Jakarta-Indonesia

I Wayan Sengara

Bandung Institute of Technology, Indonesia



SUMMARY:

Seismic design criteria derived from risk-targeted ground motions (RTGMs) for a high-rise building is investigated through integration of hazard curve from probabilistic seismic hazard analysis (PSHA) and fragility function of the building. The RTGM is defined as 1% probability of the building collapse in 50 years. The RTGMs are determined through iteration process of the risk-integral calculation such that the risk-integral reaches the target value. Most recent ground motion predictive equations for subduction, shallow crustals and background sources are adopted. Uniform hazard spectra at reference rock are derived for maximum considered earthquake (MCE) of 2% probability of exceedance in 50 years. Investigation indicated that the seismic design criteria through RTGM approach is slightly less compared to that of more conventional hazard-based MCE. Ground surface design response spectra is derived through wave propagation of RTGMs considering shear wave velocity profile obtained from combination of seismic down-hole and micro-tremor tests.

Keywords: risk-targeted, ground-motion, probabilistic, seismic hazard, response-spectra.

1. INTRODUCTION

Seismic design criteria for a high-rise building could be simply referred from applicable seismic building codes specifying spectral accelerations at referenced base-rock and corresponding Site-Class to provide design spectra. Many current seismic design criteria for buildings are based only on seismic hazard with specification on its probability of exceedance (PE). Many of the design criteria are commonly based on level of hazard of 10% PE in 50 years such as Uniform Building Codes-1997 including 2002 Indonesian seismic building codes (SNI-03-1726-2002). More recent seismic building codes such as International Building Codes-2009 are based on 2% PE in 50 years hazard.

Many recent large subduction and shallow crustal earthquakes (Great Sumatra 2004 subduction interface of $M_w=9.3$, Nias 2005 subduction of $M_w=8.7$, Yogyakarta 2006 shallow crustal, $M_w=6.3$, Pangandaran 2006, subduction of $M_w=7.2$, Indramayu 2007, subduction intraplate $M_w=7.5$, Bengkulu 2007, $M_w=8.4$, West Sumatra subduction intraplate, $M_w=7.6$, West Java subduction, $M_w=7.0$), and North Sumatra 2012, $M_w=8.6$) have risen concern on what is the potential ground shaking that could hit Jakarta city. Some of those earthquakes were felt in capital city of Jakarta. After these recent earthquakes, it is considered necessary to review and re-analyze the seismic hazard for the city, considering more recent geological and seismological input, in combination with consideration of recent advances in seismic hazard and site-response analysis (SRA). This paper presents risk-based approach for investigation to develop seismic design criteria for a high-rise building. The investigation is conducted through combining both probabilistic seismic hazard analysis (PSHA) and integrating it with fragility function of the building to result in risk-targeted ground motion (RTGM) at reference subsurface rock (Site-Class B). In addition, site-specific response analysis considering local site effect in the form of shear wave velocity profile to great depth to reference subsurface rock is also presented with recommendation on ground surface response spectra in accordance with ASCE-SEI-7-10 procedure.

2. SEISMIC HAZARD ANALYSIS

2.1. Seismo-tectonic Setting and Earthquake Source Model

The main seismic source zone is the subduction in the south and shallow crustals in the vicinity of Jakarta. Identified shallow crustal source zones that contribute to Jakarta seismicity consist of Semangko fault passing Sunda Strait, Cimandiri, and Lembang faults. All of these earthquake faults are responsible for most of the earthquake occurrences felt in Jakarta. Recently, there is a concern by some geological experts on existence of faults crossing city of Jakarta, even though this concern is not yet supported by sufficient scientific data, such as whether the fault is active or not. To accommodate this concern, then background earthquakes are included in the source model. This background earthquake model allows near field earthquakes which are not associated with definitive identified faults of potential particular maximum magnitude. **Figure 2.1.** shown seismicity and seismic source zones of the site.

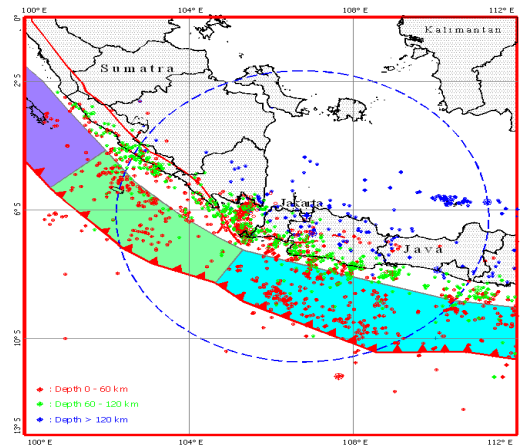


Figure 2.1. Seismicity area around site

2.2 Maximum Magnitude and Slip-rate

The maximum magnitude and slip-rate are estimated based on the evaluation of available data and tectonic of the region. The procedure identifies a reasonable maximum magnitude for the given potential seismic source and its most reasonable slip-rate in the current tectonic environment. The seismic parameters adopted in this PSHA correspond to the report on Development of Seismic Hazard Map of Indonesia for Revision of Map in SNI-03-1726-2002 by Team-9 (2010). However, since it is considered that there are large uncertainties in maximum magnitude of South Java megathrust subduction, potential of $M_{\max}=9.0$ to the Java and Southern Sumatra Interface (mega-thrust) subduction are assumed.

2.2.1 Background Seismicity Model

To account for random earthquakes on unmapped faults and smaller earthquakes on mapped faults, background gridded-seismicity model that are based on spatially smoothed earthquake rates (Frankel, et al., 1995) is considered. Background sources are based on the declustered (dependent events removed) earthquake catalog that begins in 1900. This model accounts for the observation that larger earthquakes ($M \geq 5$) occur near smaller ($M \geq 4$ or 5) earthquakes. The background gridded seismicity model are developed for both shallow crustals and deep earthquakes representing intra-slab earthquakes. Gridded seismicity included in the model is based on earthquakes at five depth intervals (shallow 0-50 km, intermediate depth 50-100 km and 100-150 km, and deep 150-200 km and 200-300 km) with each grid 0.1° . Seismic parameters for shallow background considers magnitudes that varies from 5-6.5, whereas for deep background the magnitudes varies from 5.0-7.6. Seismic parameters for each layer are identified and computed with b-value assumed = 1.0.

2.3. Ground Motion Predictive Equations

Appropriate ground motion predictive equations (GMPEs) have been adopted in the PSHA. Young's et al. (1997) and Zhao et al. (2006) are adopted to represent the subduction megathrust (interface) earthquake sources. For deep intra-slab (deep background) sources, Atkinson-Boore (2003) developed from Cascadia Intra-slab is adopted. Please note that these GMPEs are valid for ground motions to period limited to 3 seconds. GMPE from Megawati (2010) is also referred in this PSHA, because it provided ground motion period up to 10 sec. This GMPE has been included into the EZ-FRISK software and give weight of 25% each for total of 4 (four) GMPEs to represent subduction interface earthquake sources.

Next Generation Attenuation (NGA) functions are adopted for shallow crustals seismic sources and shallow background. The NGA models are elaborated in Stewart et al., 2008. The specific GMPEs from NGA that we adopt are those developed by Boore-Atkinson (2008), Campbell-Bozorgnia (2008), and Chiou-Young (2008). These three NGA GMPEs have been included in EZ-FRISK Version 7.62 that is used for this PSHA. We give equal weight of 33% for each of this GMPE.

3. RESULT OF PSHA

Two hazard levels were calculated, that is representing 50% probability of exceedance (PE) in 30 years (43 years earthquake return period), and 2% PE in 50 years (2,475 years earthquake return period) ground motions at reference subsurface rock (S_B) of Jakarta. Uniform Hazard Spectra (UHS) and de-aggregation for each hazard level were also resulted. The mean UHS for each return period is shown in **Figure 3.1**. Results of hazard curves are presented showing seismic hazard curve with each seismic source contribution to the seismic hazard for typical period of interest of $T = 1$ second, and $T = 10$ second, as shown in **Figure 3.2** and **Figure 3.3**. Result from hazard curve from **Figure 3.2**. and **Figure 3.3**. shows that for long period the subduction earthquake dominated the total hazard. This characteristic is identified from the de-aggregation analysis result for $T = 10.0$ sec shown in **Figure 3.4**., that the dominant earthquake source for long period is subduction interface.

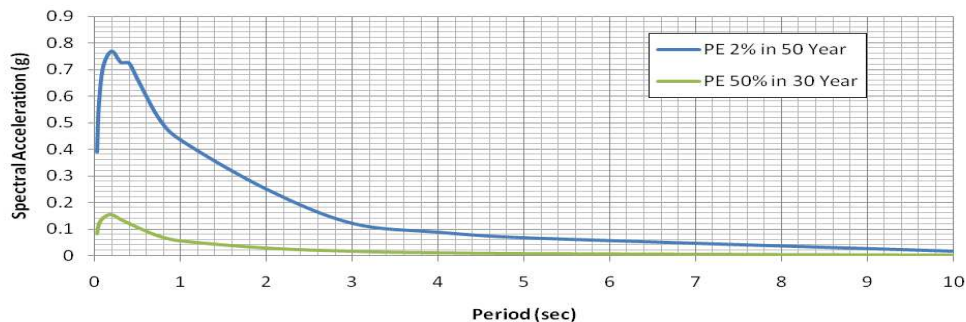


Figure 3.1. Uniform Hazard Spectra (UHS)

Results of spectral values at various periods from the PSHA would correspond to the GMPEs used in the analysis. Since the S_a values given by particular GMPE is limited to periods in the range of 3-5 seconds, then S_a for longer periods would not well estimated by the analysis. Therefore, for S_a values higher than 3.0 seconds, S_a are estimated by using an anchor value of S_a at 3.0 second to be more conservative, by adopting the following relationship:

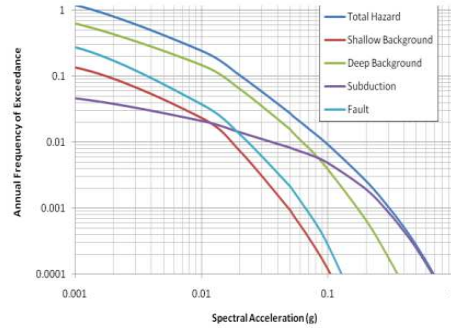


Figure 3.2. Hazard Curve for T = 1.0 sec

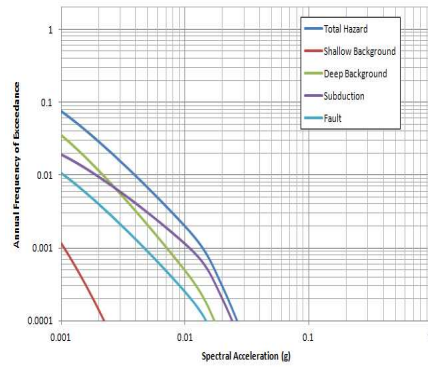


Figure 3.3. Hazard Curve for T = 10.0 sec

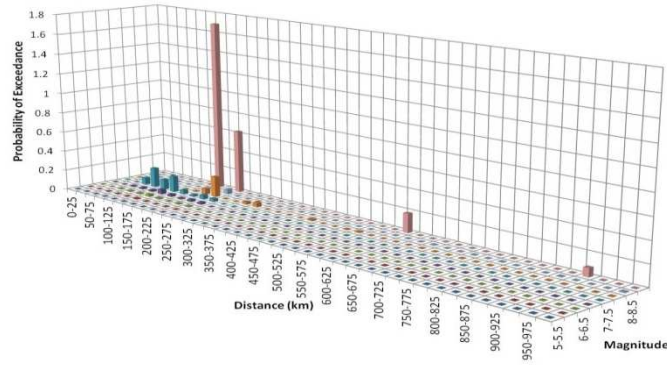


Figure 3.4. De-aggregation for PE 2% in 50 Year at T = 10.0 second

$$S_{aT} = (S_{a3.0 \text{ secs.}} \times 3.0)/T \quad (3.1)$$

where T is period of interest longer than 3 seconds.

Long period transition of the ground motion is of particular interest in this investigation since the high-rise building herein would have relatively long period. Long period transition, T_L , in this case marks the transition between the constant velocity and constant displacement segments of the fourier spectrum representing a theoretical fault-rupture displacement history. T_L is estimated from $\text{Log } T_L = -1.25 + 0.3M$, as proposed by Silva, where M is moment magnitude under consideration that would

contribute to the long period motions. In this case, with moment magnitude M in the range of 8.2 to 9, then T_L would be between 16 sec to higher than 20 sec.

4. BASE RISK-TARGETED GROUND MOTIONS

New concept in the seismic design criteria is introduced in ASCE-SEI-7-10 and PEER Guidelines for Performance-Based Seismic Design of Tall Buildings, 2010, that the seismic criteria are not only based on seismic hazard as previously adopted by many building codes, but based on probability of collapse of the buildings. The ground motions derived from this concept is called risk-targeted ground motion (RTGM). The analysis developed herein is based on MCE_R defined as 1% probability of collapse of the building in 50 years, in reference to ASCE-SEI-7-10. Since the new criteria is based on RTGM, then MCE_R needs to be derived from MCE seismic hazard and characteristics of the building in the form of its fragility. As the MCE_R is available, then design spectral values are adopted to be (2/3) of the spectral values derived from MCE_R with reference to its spectral values at various periods (in this case the spectral periods of interest is chosen to be $T=PGA$, $T=0.2$ second, $T=1$ second, $T=2$ second, $T=5$ second, and $T=10$ second). This concept is introduced for collapse prevention of the buildings.

Calculation of RTGM is done by direct integration method of multiplication of annual frequency of ground motion value $\gamma'(a)$ (site-specific hazard curve) and probability of building resistance ($P_f|a$). Uncertainty in building resistance is generally represented as building fragility. Probability of exceedance of a^* is generally formulated by the following equation (McGuire, 2004):

$$P[\text{damage} > a^*] \cong \int_a^\infty P[\text{damage} > a^* | a] * \gamma'(a) da \quad (4.1)$$

where:

$\gamma'(a)$: The annual frequency of events with amplitude a

$P[\text{damage} > a^* | a]$: probability occurred within one year

The equation is cumulative density function (CDF) that further can be replaced with normal distribution using the following equation:

$$P_F \cong \int_0^\infty \gamma(a) \frac{dP_{F|a}}{da} da \quad (4.2)$$

$$P_{F|a} = \int_0^a \frac{1}{a\sqrt{2\pi}\beta} \exp\left[-\frac{(\ln a - \overline{\ln y})^2}{2\beta^2}\right] da \quad (4.3)$$

where :

$\gamma(a)$: site-specific hazard curve from PSHA.

$\frac{dP_{F|a}}{da}$: capacity distribution.

$\overline{\ln y}$: median of logarithmic capacity x directivity factor, where directivity factor = 1.0 for PGA, 1.1 for 0.2 sec and 1.3 for 1 sec.

β : logarithmic's standard deviation.

RTGM is calculated as ground motion spectral value (a) that resulted in P_{Fa} of 1% probability of failure in 50 years through numerical integration and iterative process. This methodology is as conducted by Luco et al. (2007) by adopting generic fragility curve equation. One of essential parameters in the fragility curve equation is the value of logarithmic standard deviation, β . For this RTGM calculation, the lognormal probability density function representing the collapse fragility (probability of collapse as a function of spectral response acceleration) is defined to have 10 percent probability of collapse at particular ground motion response spectrum (a) and with a logarithmic standard deviation value of β .

Analysis and recommendation on representative β values for Indonesian buildings has been conducted through hazard analysis and probability based factor of safety by Sidi I.D.(2011). The analysis identify inherent variability of concrete compressive strength and steel reinforcement tension capacity, simplification on the field actual condition representing random phenomena in the design formulation, and random human error through reliability analysis in derivation of fragility function that considered to be representative to Indonesian condition. The analysis suggests that β values for Indonesia varies between 0.65-0.7. For development of RTGM for Jakarta site, a value of $\beta=0.65$ is adopted, assuming better performance compared to average buildings in Indonesia with $\beta=0.7$ assigned in new proposed seismic building codes of SNI-03-1726-201X. The result of Cr_s , Cr_1 to Cr_{10} is tabulated in **Table 4.1**. MCE_R is obtained by multiplying MCE with Cr values for each period. **Table 4.2**. shows the MCE_R values.

Table 4.1. Value of Cr_s , Cr_1 to Cr_{10} with $\beta = 0.65$

T(sec)	Factor Directivity	Cr
PBA*	1.00	0.985
0.2	1.10	0.976
0.75	1.24	0.913
1.0	1.30	0.903
2.0	1.30	0.904
3.0	1.30	0.929
5.0	1.30	0.916
7.5	1.30	0.955
10.0	1.30	0.943

Table 4.2. UHS, MCE, and MCE_R

T	UHS 2% PE in 50 year	MCE	MCE_R
PBA*	0.390	0.390	0.385
0.2	0.769	0.846	0.825
0.75	0.514	0.636	0.581
1.0	0.433	0.563	0.509
2.0	0.250	0.325	0.294
3.0	0.122	0.158	0.147
5.0	0.073	0.095	0.087
7.5	0.048	0.063	0.061
10.0	0.037	0.048	0.046

* PBA = peak base acceleration

The controlling magnitude and distance of dominant earthquake from de-aggregation analysis of each period of interest is adopted to generate response spectra using appropriate GMPEs. According to ASCE-SEI-7-10 and, SSRA need to be performed based on input ground motions that are scaled to base motion period by period. To accommodate this requirement, each target spectra scaled to UHS for seven (7) periods of interest (that is for $T=PBA$, $T=0.2$ sec, $T=0.5$, $T=1.0$ sec, $T=2.0$ sec, $T=5.0$ sec, and $T=10$ sec) are generated. The target spectra adopt conditional mean spectrum (CMS) method by Baker, 2011 that is built in the EZ-FRISK computer program. The generated base target spectra for scaling at those periods of interest to MCE_R values are shown in **Figure 4.1**.

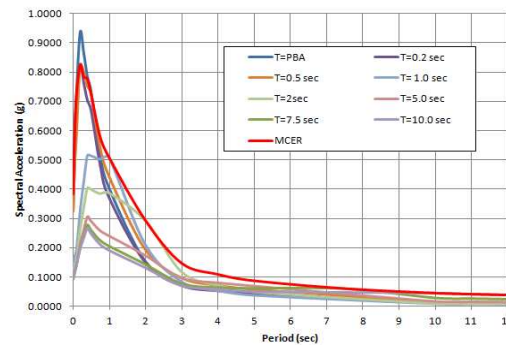


Figure 4.1. Base Target Spectra at various periods relative to MCE_R spectra

5. SPECTRAL MATCH INPUT GROUND MOTIONS

Based upon the above target spectra, synthetic input motion is generated by performing spectral-match of available strong motion records to the target spectra. Spectral-matching technique proposed by Linda Al Atik and Norman Abrahamson (2010) that is built in the EZ-FRISK 7.62 computer program (Risk Engineering, 2011) is used for the analysis. Thirty five (35) input ground motions at reference base rock (S_B) are spectral-matched to the developed MCE_R target spectra. The spectral-match to the target spectra are conducted by use of earthquake rock strong motions recorded worldwide considered to represent earthquakes based on the de-aggregation analysis.

6. SITE-SPECIFIC RESPONSE ANALYSIS

Site-specific response analysis (SSRA) require input of dynamic soil properties (shear wave velocity profile) of the site to reference subsurface base (S_B) and representative seismic input ground motions at the S_B that represent earthquake amplitudes, duration, and frequency content. According to ASCE-SEI-710, the recommended surface MCE_R ground motion response spectrum shall not be lower than the MCE_R response spectrum of the base motion multiplied by the average surface-to-base response spectral ratios (calculated period by period) obtained from the site response analyses. The recommended surface ground motions that resulted from the analysis should consider response to uncertainty in soil properties, depth of soil model, and input motions. Since the surface spectral accelerations is to be analyzed through SSRA, then the SSRA herein is conducted period by period using the generated seismic input motions at various periods described in Section 4 and Section 5.

6.1. Dynamic Soil Parameters

Figure 6.1 shows shear wave velocity data as a function of depth used for input of SSRA. The shear wave velocity profiles are obtained from combination of seismic down-hole test and ambient noise

micro-tremor survey to characterize the base-rock to ground surface site-effect to a depth of 280m, where the reference subsurface rock of $V_s \geq 760$ m/s is identified. In addition correlation of V_s from several boreholes of Standard Penetration Test (SPT) is also employed. This data is used as an input in site specific response analysis.

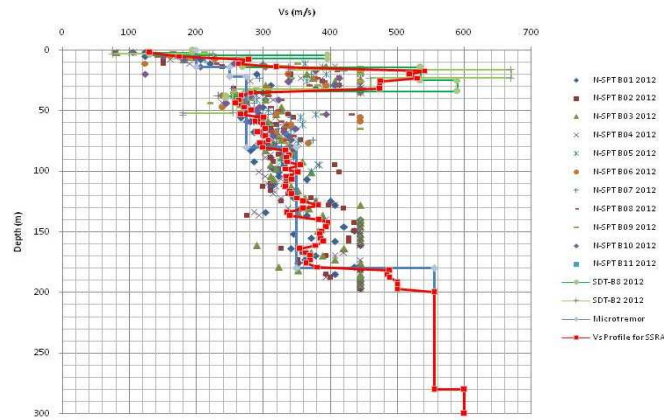


Figure 6.1. Shear wave velocity (V_s) profile for Signature Tower site based on average of 3 (three) N-SPT correlation (Ref: Sengara & Jayasaputra, 2011; Ohta & Goto, 1978; Seed & Idriss, 1981), Microtremor and Seismic Downhole Tests

6.2 Seismic Wave Propagation Procedure

Time-domain seismic wave propagation analysis from reference subsurface rock (S_B) to ground surface is conducted based on the input motions and V_s profile using computer program NERA (Non-linear Earthquake Response Analysis, Bardet dan Tobita, 2001). Shear wave propagates vertically in a one-dimensional layered system, in which the soil layers are assumed to be horizontally homogeneous, infinite horizontal extent, and subjected only to horizontal motion from the reference subsurface rock.

6.3 Design Response Spectra

Seismic wave propagation analyses were conducted for the developed input motions of the MCE_R with 5% damping and Service Level Earthquake (SLE) adopting 2.5% damping. The wave propagation considers the shear wave velocity profile to depth of baserock of Figure 6.1. Results of seismic wave propagation showing spectral accelerations at ground surface with the recommended response spectra for MCE_R , 5% damping is presented in **Figure 6.2**. Furthermore, recommended ground surface MCE_R response spectra, recommended design spectra ($S_D = 2/3 * S_a MCE_R$), and SLE design spectra is presented in **Figure 6.3**.

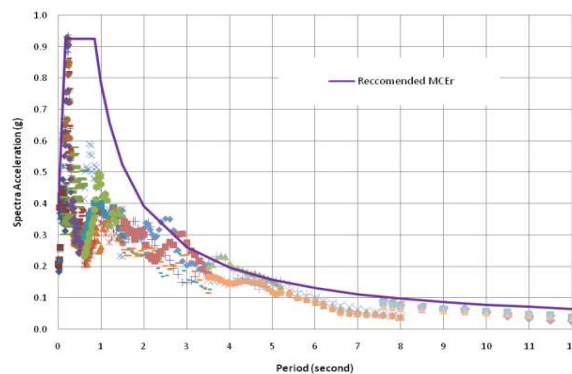


Figure 6.2. Spectral accelerations resulted from wave propagation analysis at ground surface with the recommended response spectra for MCE_R , 5% damping

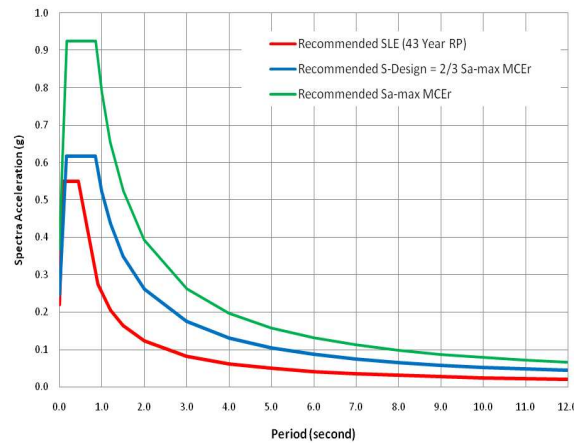


Figure 6.3. Recommended ground surface MCE_R response spectra, recommended design spectra ($S_D = 2/3 * S_a MCE_R$), and SLE design spectra

7. CONCLUSIONS

Risk-targeted based seismic design criteria development has been investigated and derived for a high-rise building in Jakarta, Indonesia. The investigation consists of derivation of hazard curve from PSHA of MCE defined as 2% PE in 50 years hazard at reference rock (S_B). Hazard curve has been developed from PSHA through comprehensive analyses considering logic-tree formulation and sensitivity analyses on maximum magnitudes of the seismic source zones. Most recent GMPEs including NGA for shallow crustals have been adopted. Risk-targeted ground motions (RTGMs) defined as ground motions at 1% probability of the building collapse in 50 years has been derived by integrating the hazard curve and building fragility with log-normal standard deviation (β) of 0.65 and identify the spectral acceleration that resulted in risk integral of 1% in 50 years. The investigation indicated that the seismic design criteria through RTGM approach is slightly less compared to that of more conventional hazard-based MCE with risk coefficient, C_R , of 0.98, 0.90, and 0.92 for 0.2, 1.0, and 5.0 periods, respectively.

De-aggregation analysis identify dominant events correspond to the level of probabilities and oscillatory periods of interest for derivation of target-spectra. The ground surface response spectra for the building has been derived based on wave propagation analyses with input motions from spectral match of target-spectra scaled to the RTGMs at MCE_R . The analyses were conducted period by period to represent the rock spectral accelerations with various oscillatory periods. The local site effect is considered by the shear wave velocity profiles obtained from combination of seismic down-hole and ambient noise micro-tremor tests to a depth of 300 meters from the ground surface. The investigation has resulted in recommendation of seismic design criteria based on methodology in accordance with ASCE-SEI-7-10.

ACKNOWLEDGEMENT

The author thankful support by PT. Grahamas Adisentosa that has provided necessary data for the investigation. The author also thank to P. Sumiartha and M.A. Yulman that have assisted in conducting some of the analysis. Contribution by Dr. G. Handayani who has provided shear wave velocity data is appreciated.

REFERENCES

Americam Society of Civil Engineers Standards, ASCE SEI-7-10, (2010), *Minimum Design Loads for Buildings and Other Structures*, Sructural Engineering Institute ASCE, Virginia, USA.

- Bardet J.P., Tobita T., (2001), "NERA, A Computer Program for Nonlinear Earthquake Site Response Analyses of layered Soil Deposits", University of Southern California.
- Frankel, A. D. (1995). Mapping Seismic Hazard in the Central and Eastern United States. *Seismological Research Letters*. **66:4**, 8-21.
- Indonesian Seismic Building Codes, SNI-03-1726, (2002), Indonesian Department of Public Work.
- Irsyam, M., Sengara, IW., Aldiamar, F., Widiyantoro, S., Triyoso, W., Natawijaya, D.H., Kertapati, E., Meilano, I., Asrurifak, M., Ridwan, M., Suhardjono, (2010): *Development of Seismic Hazards Map of Indonesia for Revision of SNI 03-1726-2002, (2010), A Summary Report submitted to Australia-Indonesia Facility for Disaster Reduction (AIFDR) and Badan Nasional Penanggulangan Bencana (BNPB)*, Institute for Research and Community Services, Institut Teknologi Bandung.
- Luco, N., Ellington, B.R., Hamburger, R.O., Hooper, J.D., and Kimball, J.K., (2007), "Risk-Targeted versus current Seismic Design Maps for Conterminous United States", *SEAOC 2007 Convention Proceedings*.
- McGuire, R.K., (2004), *Seismic Hazard and Risk Analysis*, Earthquake Engineering Research Institute (EERI) Publication No. MNO-10, Oakland, California, USA.
- Megawati K, Pan T-C (2010). Ground-motion attenuation relationship for Sumatran megathrust earthquakes. *Earthquake Engineering and Structural Dynamics*, **39:8**, 827-845.
- NEHERP Recommended Seismic Provisions for New Buildings and Other Structures, FEMA P-750/2009 Edition, Building Seismic Safety Council, Washington D.C.
- Newcomb, K.R., McCann, W.R. (1987), "Seismic History and Seismotectonic of the Sunda Arc", *Journal of Geophysical Research*, Vol. 92, No. B1, 421-439.
- Pacific Earthquake Engineering Research Center. (2010). Tall Building Initiative Guidelines for Performance Based Seismic Design of Tall Buildings. Report N0. 2010/5.
- Risk Engineering (2011), "EZ-FRISK (Software for in-depth Seismic Hazard Analysis) User's Manual", Risk Engineering Inc., Golden, Colorado, USA.
- Sengara, IW., Merati, G.W., Widiyantoro, S., Natawidjaja, D.H., Triyoso, W., Meilano, I., Kertapati, E., Sumiarta, P., Hendarto, 2009, *Final Report on Integrated Probabilistic Seismic Hazard Investigation of Indonesia (Sumatra, Java, and Nusa Tenggara)- in Indonesian*, prepared for Ministry of Research and Technology, Center for Disaster Mitigation-Institut Teknologi Bandung, Indonesia.
- Sengara, IW., 2009, "Development of Earthquake Scenario for Three Different Sites within City of Jakarta", Earthquake Geotechnical Engineering Satellite Conference XVIIth International Conference on Soil Mechanics & Geotechnical Engineering, Alexandria, Egypt
- Sengara, IW., and Jayasaputra, U., 2010, Study of Empirical Correlations to Estimate Shear Wave Velocity based on MASW, Seismic Downhole, and Soil Investigation Data, Research Report, Geotechnical Engineering Laboratory, Inter University Center for Engineering Science, Institut Teknologi Bandung.
- Sengara, IW., Sumiarta, P., Handayani, G., and Yulman, M.A., 2012, "Report on Probabilistic Seismic Hazard and Site-Specific Response Analysis to Derive Seismic Design Criteria for Signature Tower – Jakarta, a Report submitted to PT. Grahama Adisentosa, PT Georeka Indonesia.
- Stewart, J.P., Archuleta, R.J., and Power, M.S., (2008), *Earthquake Spectra*, The Professional Journal of the Earthquake Engineering Research Institute, Special Issue on the Next Generation Attenuation Project, Volume 24, Number 1,
- Youngs, R. R., Chiou, S. J., Silva, W. J., Humphrey, J. R., (1997), "Strong Ground Motion Attenuation Relationship for Subduction Zone Earthquake", *Bulletin of Seismological Society of America* Vol. 68, No. 1.
- Zhao, John X., Jian Zhang, Akihiro Asano, Yuki Ohno, Taishi Oouchi, Toshimasa Takahashi, Hiroshi Ogawa, Kojiro Irikura, Hong K. Thio, Paul G. Sommerville, Yasuhiro Fukushima, and Yoshimitsu Fukushima. (2006). Attenuation Relations of Strong ground Motion in Japan Using Site Classification Based on Predominant Period. *Bulletin of the Seismological Society of America* **96: 3**, 898-913.